

Number 4

May 31, 1938

A STATISTICAL STUDY OF THE RATTLESNAKES

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V\* HEAD DIMENSIONS

Table of Contents

Introduction . . . . .	2
Measurement Methods . . . . .	3
Sexual Dimorphism . . . . .	3
Nature of Head-to-Body Relationship . . . . .	5
Comparison of Straight Line and Parabolic Regression . . . . .	7
Example Colubrid Head Proportions . . . . .	9
Dispersion in Head Length--Variation with Body Length . . . . .	11
Extent of Dispersion--Limited Age Groups . . . . .	12
Character of Dispersion--Complete Age Series . . . . .	15
Head Length as a Diagnostic Character . . . . .	20
Example Taxonomic Problems . . . . .	22
Validity of Head Length as a Diagnostic Character . . . . .	24
Short Cut Methods . . . . .	25
Use of L/H Ratio . . . . .	27
Dwarfed Forms . . . . .	29
Effect of Ultimate Length on Species-Difference Calculations . . . . .	34
Effect of Ultimate Length on Dispersion . . . . .	36
Sexual Dimorphism in L/H . . . . .	36
Species Differences--General Discussion . . . . .	39
Width and Depth . . . . .	45
Summary and Conclusions . . . . .	51

\* Previous sections of this paper have appeared as follows: I, Introduction; II, Sex Ratio in Rattlesnake Populations; III, Birth Rate; Occasional Papers S.D.Soc.Nat.Hist., No.1, pp.1-24, figs.1-2, tables 1-4, Aug.10, 1936; IV, The Growth of the Rattlesnake; Occasional Papers S.D.Soc.Nat.Hist., No.3, pp.1-56, figs.3-6, tables 5-16, Dec.15, 1937.

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## V HEAD DIMENSIONS

### Introduction

The head length of a snake is known to be a diagnostic character of some value and as such has often been cited in species descriptions and in taxonomic comparisons. However, it is a quantity which changes with growth, during the life of each individual, and therefore a basis of comparison other than mere linear measurement must be devised. Usually this has taken the form of a proportion--the ratio of the head length to the body length over-all; or its reciprocal, the number of times the head length is contained in the body length. It is the purpose of this study to determine the value of this character in species diagnosis, at least as it applies to the rattlesnakes. In such an investigation we must consider the accuracy (and therefore the validity) of measurements. We must find how the head size varies with the body size during growth--whether this relationship can be expressed as a simple ratio, as has often been assumed to be the case. We must examine the dispersion of this proportionality within a species to find whether intraspecies variation is so great as to limit or invalidate comparisons between species. The presence or absence of sexual dimorphism must be ascertained.

In addition to the possible taxonomic value of head length studies, they afford a basis for the consideration of variations in fang length and venom yield, which are matters of some practical importance in the snake bite problem. I expect, in a subsequent section of this series, to report upon correlations between head size, fang length, and venom secretion.

This study of the head length variations among the rattlesnakes originally contemplated the preparation of a table comparing the several species and subspecies statistically, drawing attention to those which deviate conspicuously from the rattlesnake mode. Examples were to be presented, showing how species differences in this characteristic might be verified.

These simple objectives proved far more elusive than was expected. The difficulty of dealing with a quantity, which not only varies between individuals, as is to be expected in any group of animals, but which fails to remain constant with respect to any single individual during his lifetime, became increasingly apparent as the work progressed.

In the taxonomic study of a genus of snakes, head length is only one of many characters which may be employed as differential criteria. In most cases it will not be found of critical importance, although in a few instances it may afford finality in determining differences and relationships. In view of these facts, the space which is here

given to the development of head length statistics is not to be interpreted as an indication of the relative value which the writer attaches to this character. But it appeared to offer a useful example of how the proportion of a body part may be handled statistically. In addition it seemed worth while to investigate fully, as a typical example, the nature of the variation of head length within a single species. This is my reason for having worked out the complete trends in the Platteville and Pierre series of Crotalus viridis viridis, as subsequently presented. But as a survey of a purely taxonomic criterion, this amount of detail is not justified.

### Measurement Methods

The head length, as used in the present study, is the distance between the front face of the rostral and the posterior end of either mandible; this, it is found, can be calipered with reasonable accuracy. This dimension, although at a slight angle with the center-line of the body, differs only in a minor degree from the distance between the rostral and the mid-point of a line joining the posterior ends of the mandibles, which might be considered the true length of the head.

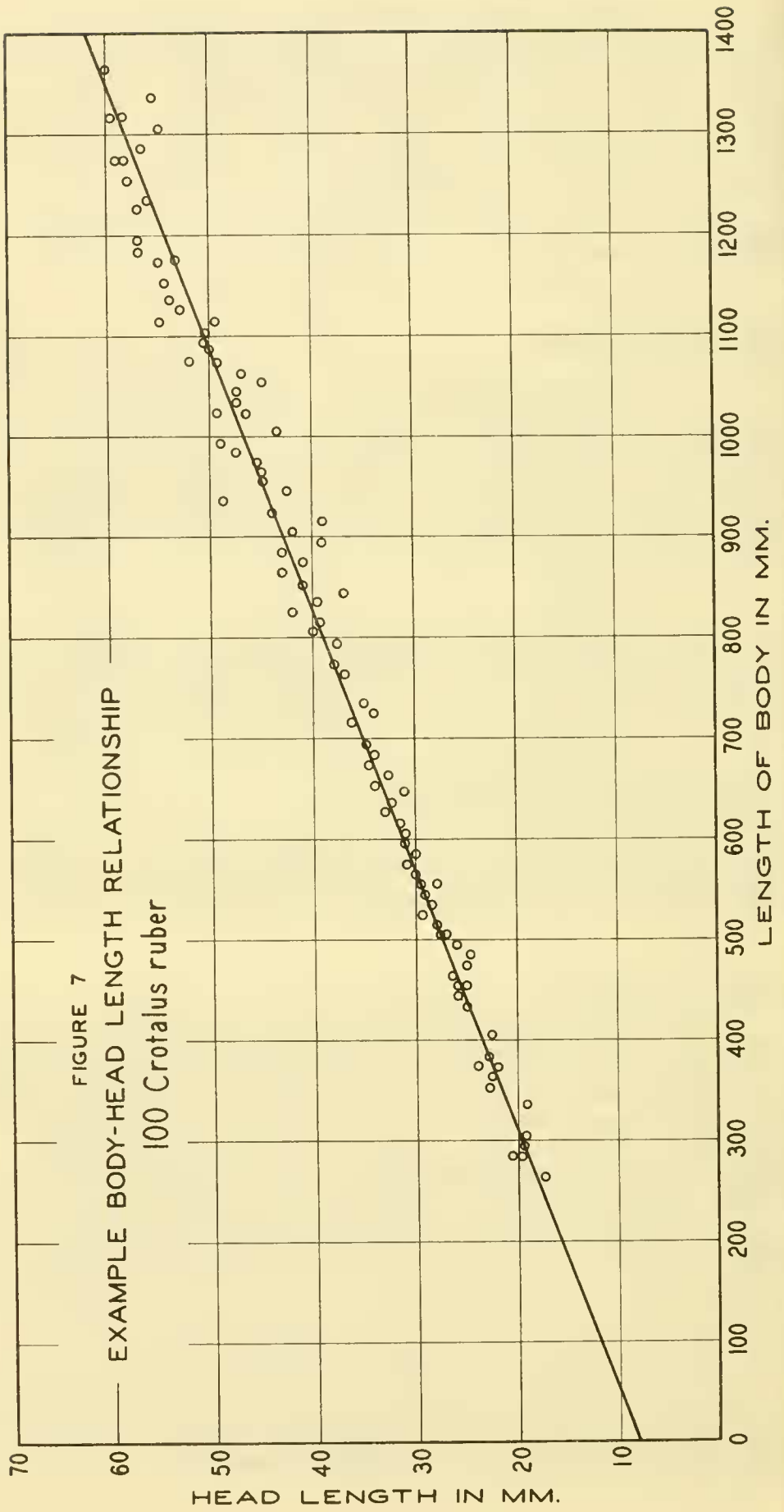
Head length, as above defined, is affected by preservative somewhat more than body length. In a series of specimens in which the body length was found to decrease in alcohol by 2 per cent, the head length was decreased by an average of 6.8 per cent. It is therefore desirable to measure specimens before they have set in the preservative, although this is not as easy, because of the soft tissues, as it is after the head has hardened. In any case where the highest accuracy is required, it is necessary to handle all comparative material in the same manner, that is, either freshly killed, or after setting in preservative. In the present investigation pre-set measurements were frequently used, especially in the large homogeneous series from which the character of variation has been determined.

### Sexual Dimorphism

In coördinating the statistics of head length it is advisable to investigate sexual dimorphism first, since, if there be none, the subsequent problems will be simplified. To investigate this question a determination was made (separately for each subspecies) of the average size of the head for each size-class of body\* in series of cinereous, lucasensis, ruber, scutulatus, viridis, lutosus, and organus. These comparisons were made only between size-classes within the adult range, where sexual dimorphism, if present, would naturally be manifest. It was found that such variations as were apparent, as frequently showed one sex to have a larger head as the other; the variations seemed to be dictated entirely by chance. These series totalled 210 size-classes, involving 1846 snakes. In these 210 classes it was found that the male heads averaged

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\* Body size-classes were taken by 10 mm. increments; for example all the snakes of a subspecies from 740 to 749 mm., inclusive, were grouped in a single size-class.



larger in 90, the females were larger in 108, and in 12 classes the sexes were equal. Thus we conclude, with respect to these species and subspecies, that there is no sexual dimorphism in head length at equal body lengths. A more conclusive test of this equality, using viridis as an example, and a probable deviation in the case of cerastes are discussed on p. 36, subsequent to the development of certain methods of analysis.

### Nature of Head-to-Body Relationship

As is usual in considering the importance of diagnostic characters, there are two phases to be investigated: first the consistency (or its opposite, dispersion) of the character within a single species; secondly the differences between species. The extent of the first determines the relative importance of the second.

That there should be a definite correlation between head size and body length is obvious; the problem concerns the nature of the correlation, whether linear or of higher degree, and how closely individuals adhere to the regression line.

As an initial visual survey, the head-length and corresponding body-length coördinates of several series of specimens, each series representing a different species or subspecies, were set up on rectangular cross-section paper. In each series the points are found to lie approximately on a straight line. No definite and consistent curvilinear departure is noted; for while some series appear to bow upward slightly, an equal number have a slight sag. Although there is some scatter the adherence to the regression lines is fairly close. Thus the relationship seems to be simple and linear. However the regression lines do not, in any species, pass through the origin, the intersection with the line  $H = 0$  being always on the negative side; the equation therefore is of the form  $H = aL + b$ ; and, because of the presence of the constant positive term b, we know at once that the head length does not bear a constant proportionality to the body length throughout life.\* Furthermore, b is relatively of considerable magnitude, so that this deviation from a constant ratio is marked--juvenile rattlers have proportionally larger heads than adults. For example the equations of the several viridis subspecies all approximate  $H = 0.035L + 7.5$ , where H and L are expressed in millimeters. Thus a juvenile 300 mm. long has a head length averaging 18 mm., while the head of a 1000 mm. adult measures about 42.5 mm. The juvenile head length is 6 per cent of the body length; the adult only 4.25 per cent. This proportionately larger juvenile head is a condition common to many animals.

For the better visualization of the relationships above set forth, reference is made to Fig. 7 showing, on rectangular coördinates, the head-body correlation in 100 C. ruber evenly distributed amongst juveniles, adolescents, and adults, but otherwise chosen at random from a large

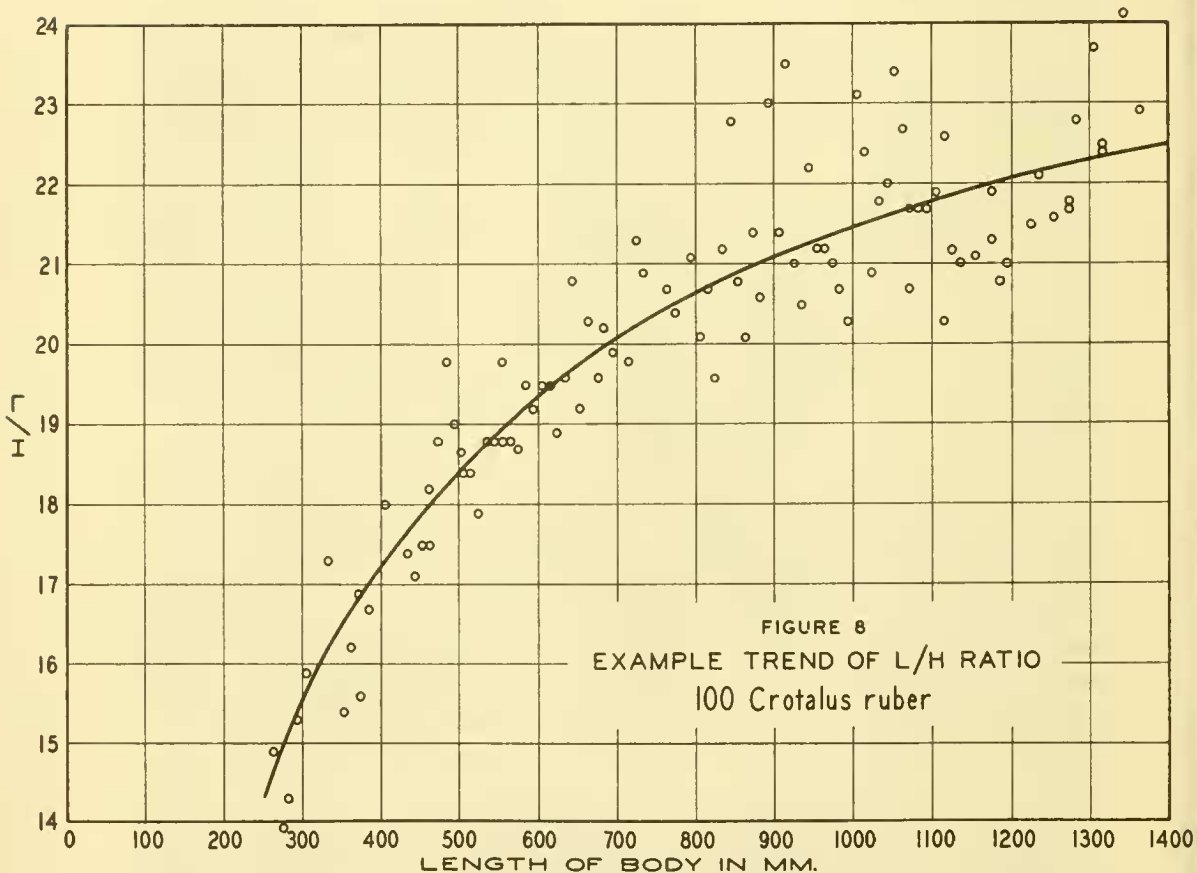
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\* For, if  $H = aL + b$ , then  $H/L = a + b/L$ ; therefore the ratio of the head to the body is not constant but changes with L. Lower case algebraic quantities appearing in the text outside of equations are underlined for clarity, as is b above.

series. Attention is directed to the facts previously discussed: (1) a straight line fits the situation quite well; (2) this line does not pass through the origin, that is, the point where  $H = 0$  when  $L = 0$ ; (3) the adherence to the regression line is fairly close, the scatter not being excessive.

Also Fig. 8 has been prepared from the same 100 specimens of *C. ruber*. This shows how  $L/H$  changes as the snakes age, and how futile it is to make interspecies comparisons of  $L/H$  ratios, unless the material compared be restricted to a narrow and comparable length-range.

One might suppose this type of relationship between head and body length to be the result of the shortening of the rattlesnake tail by the rattles--that if the rattlesnake had a normal tail the increased body length would produce a constant ratio between  $H$  and  $L$ . However such is not the case. To produce a constant ratio between  $H$  and  $L$ , a constant,  $b/a$ , must be added to  $L$ ; which means that regardless of the size of the snake we must assume that the tail was foreshortened in a fixed amount by the



presence of the rattle. This is obviously not what has occurred. Whatever shortening may have been produced through the replacement of the usual tapered tail by the rattle, it was in some degree proportional to the size of the snake, as elementary comparative studies of tail lengths in Crotalus and Agkistrodon will show. Certainly if a large rattler 1000 mm. long, with a tail 75 mm. long, lost 180 mm. by shortening, it is impossible that a juvenile 300 mm. long with a 22 mm. tail could have similarly lost 180 mm. Yet something of this nature would be required to indicate derivation from a constant relationship between head and body.

The accuracy of a straight-line relationship of the form  $H = aL + b$  has been questioned by some with whom the matter has been discussed. They point out that, at zero body length,  $H$  has a value of  $b$ , an obvious impossibility. This I grant, but it is not claimed that the equation covers the prenatal as well as the postnatal stage. What form the growth curve takes in the prenatal stage I do not know; I merely suggest that the straight line closely represents the relationship during life. Plotting a number of species on log-log coördinates we find curves to result in almost every series; thus the frequently used relative-growth equation  $Y = cX^k$  does not represent the situation as well as the simpler linear equation. Even two consecutive straight-line sections on log-log coördinates, such as would indicate a change in the rate of proportionate growth at some point in the life cycle (adolescence for example) do not seem to be applicable here.\*

#### Comparison of Straight Line and Parabolic Regression

I do not mean to state that it is impossible to find a parabolic curve to fit the head-body relationship with a fair approximation. Taking, for example, the Platteville series of 833 specimens of Crotalus viridis viridis, we find that the equation  $H = 0.279L^{0.724}$  fits the situation moderately well, although the simpler and more practicable equation  $H = 0.0355L + 7$  fits considerably better, over the complete range from birth to maximum size.

To make certain of this matter of relative appropriateness of formulas, 19 representative species or territorial series were plotted on log-log paper. In general the resulting regression lines showed a distinctly greater tendency to curvature than was the case with the same data plotted on rectangular coördinates. Only in one or two cases out of the 19, where uniform coördinates resulted in regression lines perceptibly bowed upward in the center, did the log-log paper tend to straighten the line; in most cases logarithmic coördinates produced a curve having a central sag, with considerably greater deviation from a straight line than the quadrille ruling. However, for those who prefer equations of the parabolic form, the following table gives the constants for each species in the equation  $H = cL^k$ , which produce an approximate fit, although the formulas will usually give juvenile and adult heads lower than actuality, while the adolescents will be high.

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\* See Julian Huxley, Problems of Relative Growth; New York, 1932, p. 10.

Constants in the Equation  $H = cL^k$

<u>Species or Subspecies</u>	<u>c</u>	<u>k</u>
C.d. durissus	0.330	0.715
C. enyo	0.339	0.680
C.m. molossus	0.240	0.764
C. adamanteus	0.241	0.775
C. cinereous	0.300	0.722
C. lucasensis	0.339	0.708
C. ruber	0.275	0.741
C. scutulatus	0.196	0.634
C.v. viridis		
Platteville series	0.279	0.724
Pierre series	0.343	0.692
C.v. lutosus	0.310	0.703
C.v. oreganus		
San Diego County	0.315	0.717
C.m. pyrrhus	0.226	0.762
C. cerastes	0.159	0.817
C.h. horridus	0.374	0.684
C.l. klauberi	0.230	0.748
C.t. pricei	0.196	0.778
S.m. streckeri	0.422	0.657
S.c. catenatus	0.663	0.584

It will be observed that there are considerable differences in the constants of closely related species--differences which do not occur to a similar extent in the constants of the straight-line formulas, as will be subsequently shown. This is because of the major effect of the juveniles in determining a parabolic equation, and the considerable changes in the constants with small changes in the slope of the curve. In reality the statement of the third figure in these constants gives an aspect of accuracy which is not justified by the facts.

One minor advantage in the use of an equation of the form  $H = cL^k$  lies in its convertibility into an equation of  $L/H$  in terms of  $L$ , while the straight line form  $H = aL + b$  is not convertible, as pointed out before. Thus from  $H = cL^k$  we derive the equation  $L/H = c^{-1}L^{1-k}$ . For example in the Platteville series, if  $H = 0.279L^{0.724}$ , then  $L/H = 3.58L^{0.276}$ . But this is to be considered only an approximation. In general there appears to be no advantage, either of accuracy or workability in adhering to the more involved parabolic formula, consequently the subsequent discussion is based on the more accurate straight-line relationship.

Of course there is no theoretical reason why rattler  $H$  on  $L$  regression lines should conform either to the straight line  $H = aL + b$  or the simple parabola  $H = cL^k$ . They might equally well follow some curve of higher degree lying between the two.\* But as I have said, plotting many

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\* To determine the nature of the curves followed by those species which (probably due to the exigencies of sampling) diverge from straight lines, the two showing the most conspicuous deviations were selected for analysis. These are cinereous which sags slightly, and c. catenatus which bows upward in the center. By the usual methods of curve fitting both are found to adhere to second degree parabolas very closely. As the curves are quite flat, the  $L^2$  compo-



series results in deviations on both sides of a straight line, in about equal numbers; so that I am convinced that the straight line gives the nearest approach to a universal fit. With respect to one species the straight line is shown analytically to give the best fit (p.16).

### Example Colubrid Head Proportions

Before leaving the matter of the suitability of certain types of equations to represent this relationship, I might mention some results of a similar investigation of several colubrine snakes. Having determined that the rattlers rather unexpectedly followed a straight line regression in the head length relationship, it was natural to check the situation in other genera to find if this were a common or universal relationship amongst the snakes. Preliminary results indicate that it is not. Of six species tested, two seem to follow straight lines. Arizona elegans occidentalis, based on 64 specimens, adheres closely to the equation  $H = 0.022L + 6.5$ ; while 82 specimens of Lampropeltis getulus californiae give  $H = 0.024 + 6.3$ . But 4 other colubrids selected at random all show distinct sags when plotted on quadrille ruled paper and essentially straight lines when plotted on semi-log coordinates. Hence their equations are of the form  $H = mn^L$ , where  $m$  and  $n$  are constants. In using this equation it is best to express  $L$  in meters, rather than in millimeters, since to do otherwise makes  $n$  unwieldy in form. The results secured in the cases tested were as follows:

<u>Species</u>	<u>Number of Specimens</u>	<u>m</u>	<u>n</u>
Trimorphodon vandenburghi	14	7.35	4.52
Phyllorhynchus d. perkinsi	70	6.25	5.60
Masticophis f. frenatus	36	12.8	3.28
Masticophis lateralis	23	11.2	3.70

For example the head length relationship in Trimorphodon vandenburghi may be written  $H = 7.35(4.52)^L$ ,  $H$  being the head length in millimeters and  $L$  the length overall in meters.

Whether there is anything significant in the fact that some species appear to follow a straight line, while an exponential equation best suits the others, I am not prepared to say. This offers an interesting field of research. Possibly some intermediate form of curve, falling between the two, may be more universally applicable. In any case it is interesting to note that in none of these colubrids does the head length have a constant ratio to body length. Most colubrids are considerably more difficult to measure with accuracy than such broad-headed snakes as the rattlers.

nents are small. The straight lines of best fit are also presented for comparison:

<u>C. cinereous</u>	Parabola	$H = 0.00000432L^2 + 0.0306L + 9.5$
	Straight line	$H = 0.0351L + 8.7$
<u>S.c.catenatus</u>	Parabola	$H = -0.00000504L^2 + 0.0344L + 8.6$
	Straight line	$H = 0.0302L + 9.3$

It will be noted that the direction of the deviation from the straight line is indicated by the sign of the  $L^2$  term.

Table 17

CORRELATION OF HEAD AND BODY LENGTH: PIERRE SERIES OF 715 SPECIMENS OF *C.v.viridis*

## Head Length in Millimeters

	16 to 17.9	18 to 19.9	20 to 21.9	22 to 23.9	24 to 25.9	26 to 27.9	28 to 29.9	30 to 31.9	32 to 33.9	34 to 35.9	36 to 37.9	38 to 39.9	40 to 41.9	42 to 43.9	44 to 45.9	Total
250-279	4															4
280-309	8	10														18
310-339	4	54														58
340-369		27	34													61
370-399		2	15	1												18
400-429			1	2	1											4
430-459			4		4	1										5
460-489			7		2	2										9
490-519			12		2											14
520-549			4		12	3										19
550-579			1		11	5		1								18
580-609					9	18		4								31
610-639					1	18		11								30
640-669						9		20	1							30
670-699						3		26	12							41
700-729								14	21	1						38
730-759								4	19	7						30
760-789							2		11	17						30
790-819									6	24	2					56
820-849									1	18	24	2				46
850-879									1	3	20	5				46
880-909									1	4	13	14	2			32
910-939									1		10	18	1			38
940-969											10	10	7		3	20
970-999												1	4			5
1000-1029												1	5			10
1030-1059													4			1
1060-1089													1		1	3
Total	16	93	50	3	29	38	58	80	72	74	91	71	31	8	1	715

Body Length in Millimeters

Having found an exponential equation to fit the head-body relationship in certain colubrids a test was made on several rattlers (the three species showing the greatest sag when plotted on rectangular coördinates) to see if, in their cases, an equation of this type might not be more suitable than a straight line. This was found not to be the case; even in these extreme instances adherence to a straight line was closer than to an exponential formula of the type followed by these colubrine snakes.

#### Dispersion in Head Length--Variation with Body Length

We now return to the rattlers and to a more detailed study of the straight line of best fit, and the closeness of adherence of individual specimens to this regression line. The coefficient of correlation was determined in three large homogeneous series, the Cape San Lucas series of Crotalus lucasensis and the Platteville and Pierre series of Crotalus viridis viridis mentioned in previous sections of this paper. The correlation table of the latter group is set forth as an example in Table 17. The results follow:

	<u>Lucasensis</u>	<u>Viridis</u>	
		<u>Platteville</u>	<u>Pierre</u>
Number of specimens	247	833	715
Coefficient of correlation (r)	0.831	0.989	0.988
Standard error of estimate, mm.	4.17	1.03	1.10

Despite the relatively high coefficient of correlation, thus determined, I do not consider the standard error of estimate to be particularly indicative of the value of head length as a diagnostic character: first because the value of  $r$  will depend too much on the distribution (in length) of the available specimens;\* and, secondly, because the method gives an equal value to all deviations in terms of absolute measurement. By this I mean that a deviation in head length of 3 mm. from the regression line at a body length of 300 mm. has the same weight in determining the value of the standard error of estimate as a deviation of 3 mm. at a body length of 1000 mm. But (using as an example the equation  $H = 0.035L + 7.5$ ) in the one case the deviation from normal is 16.7 per cent, whereas in the other it is only 7.1 per cent. I see no reason to assume that if a snake differs 3 mm. in head length from the normal of his species as a juvenile, he will continue to differ by this absolute amount as an adult, when 3 mm. will have become a relatively smaller deviation. Rather it would be more logical to assume a constant proportional deviation; the snake deviating 3 mm. in head length, or 16.7 per cent, at a body length of 300 mm. will also probably deviate about 16.7 per cent, or 7.1 mm., when he has grown to a body length of 1000 mm.

This assumption might be tested if we had two

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\* As an example observe the following variations in the value of  $r$ : Platteville series--entire series 0.989, juveniles 0.828, adult males 0.943, adult females 0.906; Pierre series--entire series 0.988, juveniles 0.881, adult males, 0.943, adult females 0.926. The limited age groups always have a lower correlation than the entire series, since the scatter is proportionately increased.

large series of specimens available, all of one, for example, being exactly 300 mm. long, the other all 1000 mm. These are not at hand; if they were we could at once determine the coefficients of variation which we are seeking and thus obviate the assumptions which we are trying to substantiate. But we do have available some fairly numerous concentrations within several juvenile and adult groups. Using these we may test certain homogeneous juvenile groups falling within a 10 mm. body-length range, and adult groups within a 30 mm. range, and determine their respective coefficients of variation. It appears fair to have the ranges cover approximately the same percentages of the length over-all. Such a calculation is equivalent to assuming that the heads are without change in size while the body makes this small growth. This assumption will lead to a slightly higher value of the coefficient of variation than the true figure. The results of such a determination follow:

		<u>Number of specimens</u>	<u>Length range in mm.</u>	<u>Coefficient of variation in per cent</u>
<u>Juveniles</u>				
San Patricio	<u>cinereous</u>	40	310-319	2.74
Platteville	<u>viridis</u>	37	270-279	3.35
Pierre	<u>viridis</u>	27	320-329	2.31
San Diego Co.	<u>oreganus</u>	27	330-339	2.76
<u>Adults</u>				
Cape	<u>lucasensis</u>	27	1110-1139	4.08
Platteville	<u>viridis</u>	65	760-789	3.76
Pierre	<u>viridis</u>	57	800-829	3.16

It will be observed that there is no decrease in the coefficient of variation--if anything an increase is shown in the adults over the juveniles.\* The same conclusion is evident in all species, from a visual inspection of the scatter about the regression lines. Thus it is indicated that during ontogeny any deviation in head length from the normal is more likely to be maintained at a constant percentage than at a constant absolute value. The subsequent calculations are continued on this assumption, and we abandon the usual method of computing the coefficient of correlation and the standard error of estimate as being of no particular value in the present instance. It is our purpose to devise a statistic which gives a clearer and more useful picture of the dispersion.

#### Extent of Dispersion--Limited Age Groups

It has been stated that the value of the head

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\* Some might presume that the increase in the coefficient of variation of the adults as compared to the juveniles is the result of taking a wider length-range (30 mm.) in the former group, as compared to 10 mm. in the latter. This is not so. For example, taking the Platteville adults having the range 760 to 789 mm. and dividing these into three groups having 10 mm. increments, we find the several separate coefficients of variation to be 3.97, 3.68 and 3.31 per cent. The average, 3.65, is not greatly different from the figure 3.76, arrived at by taking the 30 mm. zone as a single unit.

length as a diagnostic character depends on the relative dispersion within a homogeneous group, as compared with the difference between the means of two groups representing separate species or subspecies. In using the assumption of constant percentage deviation, as previously tested, we first determine the regression line for the group by the method of least squares\* or other suitable means. We then use this equation to transpose each measured head size to the equivalent head size which that individual would probably have at some arbitrarily selected standard length.<sup>φ</sup> If enough specimens are available it is always advisable to employ only those within a relatively narrow length-range. By so doing we eliminate, or minimize, the increased variance which might result from any unsuspected deviation of the regression curve from a straight line, or from an inaccurate slope in the regression line; for with a limited length-range the specimen is translated only a short distance along the line.

Thus we secure an array of equivalent measurements from which, not only the dispersion constants can be computed, but the nature of the dispersion may be ascertained. For example, 185 juvenile specimens of C.v. oregonus from San Diego County, varying in length from 260 to 398 mm. were measured and the head dimensions were reduced (by the application of the equation of H on L determined from these individuals) to a standard body length of 330 mm., and the statistics of dispersion were then determined. In a similar manner other groups were investigated, including the adult series of viridis from Pierre, adult lucasensis, and the San Patricio juvenile cinereous. The results are set forth in Table 18.

In these limited geographical groups the head size is seen to be quite consistent. The extremes are not to be taken too seriously; they often represent errors in measurement, injured specimens, or distortion in preservation. It is important to note that half the specimens (as indicated by the semi-interquartile range in per cent) are likely to fall within  $\pm 3\frac{1}{2}$  per cent of the mean. We find again, in comparing the juvenile and adult groups, that deviations (as indicated by the coefficients of variation) are similar on a percentage basis, rather than on an absolute basis; thus we visualize the dispersion surface as widening with increased body length. If we assume, as is indicated by graphical studies of dispersions about the H on L lines of best fit, that the dispersions in other species are similar in degree to the four developed in Table 18, the head size may be of real value in diagnosis, particularly if a moderate number

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\* The method of least squares, being based on absolute, not proportionate deviations, may introduce a slight error, but the correlation is so high that it may be neglected. (See p.20) If one prefers the parabolic approximation,  $H = cL^k$ , in its straight line form  $\log H = k \log L + \log c$ , in deriving the standard error of estimate, deviations proportionate to size are automatically assumed.

<sup>φ</sup> The deviation varies in proportion to  $L + b/a$ , not in proportion to L alone. Thus if  $h$  represents the deviation at length L and we desire to find the equivalent deviation  $h_0$  at standard length  $L_0$  we have  $h_0 = h(L_0 + b/a)/(L + b/a)$ . As  $L_0 + b/a$  is a constant, it is seen that deviations vary with  $L + b/a$ . For an example computation of the reduction of head length to a standard see p.22.

Table 18

## DISPERSION CONSTANTS OF HEAD LENGTH REDUCED TO STANDARD BODY SIZE

	Juvenile San Diego oreganus	Juvenile San Patricio cinereous	Adult Pierre viridis	Adult lucasensis
Number of specimens	185	139	154	180
<u>Length over-all:</u>				
Length range, mm.	260-398	274-344	800-899	850-1139
Assumed standard body length, mm.	330	310	850	1000
<u>Statistics of head length reduced to standard body length:</u>				
Mean head length, mm.	20.382	19.468	36.603	46.372
Probable error of the mean, mm.	±0.039	±0.027	±0.074	±0.089
Standard devia- tion, mm.	0.787	0.476	1.356	1.765
Coefficient of va- riation, per cent	3.87	2.44	3.70	3.81
Extreme range, mm.	18.2-22.1	18.4-20.7	31.1-39.2	40.3-51.7
Interquartile range, mm.	19.9-20.9	19.2-19.8	35.7-37.5	45.2-47.6
Semi-interquartile range, per cent	±2.61	±1.65	±2.50	±2.57
Variation of L/H within the inter- quartile range	16.6-15.8	16.1-15.7	23.8-22.7	22.1-21.0

of specimens be available. A character having a coefficient of variation usually below 5 per cent does not compare unfavorably with others used in taxonomy, as shown in Table 14.

While discussing the extent of the variation in head length at any fixed body length, it should be pointed out that at least a part of this variation may not be a mere random divergence in the proportional parts of head and body; on the contrary, it may result from an attempt upon the part of nature to produce a uniformity of L/H at corresponding ages. For, as is subsequently shown (p.36), morphological homogeneity at corresponding ages, within a population of snakes growing to different ultimate lengths (a condition common to all populations), will in itself produce a scatter about the regression line of H on L just as we find here. In other words, this scatter may be attributed to a certain type of uniformity rather than nonuniformity.

#### Character of Dispersion--Complete Age Series

The data contained in Table 18 were based on snakes of limited body-length ranges, to be assured of a straight regression line. As a final survey of the nature and consistency of the head-body relationship we proceed to investigate our two largest available series (the Platteville and Pierre series of C.v. viridis) from birth to ultimate adult size, using in each case the proportionate method of reducing head size to the equivalent size at a standard body length. In other words every specimen in the series is reduced to a single standard body length; the resulting head lengths are entirely comparable, and may be gathered in a statistical array for computation of the character and degree of dispersion. Standard tests for linearity of regression may be made. Finally, by the chi-square test, the resemblance of this cross section of the dispersion surface to a normal curve may be investigated.

The Platteville series of 833 specimens was checked analytically; but in order that the nature of the dispersion might be visualized from juvenile to adult, a graphic as well as an analytic study was made of the 715 specimens of the Pierre series of viridis. The regression line having been determined from a correlation table, the area immediately adjacent thereto was divided into a central zone with eight equal zones (i.e., with equal intercepts on the H-lines) on either side. The zones widen proportionate to  $L + b/a$ , so that all points having the same per cent deviation from the regression line (rather than the same absolute deviation) fall within the same zone. The total points within each zone were counted and the results tabulated. Thus, there was secured an average cross-section of the dispersion surface as intercepted by a plane parallel to the H-axis and perpendicular to the L-axis.

A study of the graphical presentation of the results derived from these 715 specimens, which is not here reproduced, as a very large sheet would be required for the purpose, gives impressive visual verification of the assumption that dispersion is not uniform in terms of absolute measurement, but rather is proportionate to  $L + b/a$ , with a slight increase in variability in the last adult stages.

In the analytic study of the two series, correla-

tion tables (see Table 17 for example) were first prepared in order to determine the constants of the regression equations. These were then used, in the manner previously outlined, to reduce all head lengths to a standard body length of 900 mm. This length was selected as representing a fairly large adult, and is employed in order that the variations in head size might be visualized. The variations at any other body size may be easily determined, using the regression equations and the values of the coefficient of variation. These, in fact, constitute the important result of the computation. The statistics follow:

	<u>Platteville series</u>	<u>Pierre series</u>
Number of specimens	833	715
Regression constants (in the equation $H = aL + b$ )	<u>a</u> 0.03553	0.03350
	<u>b</u> 6.968	8.363
Mean length of head, mm. (at standard body length of 900 mm.)	38.94 ± 0.0317	38.51 ± 0.0347
Interquartile range, mm.	38.02 to 39.86	37.58 to 39.44
Standard deviation, mm.	1.359	1.376
Coefficient of variation, per cent	3.49	3.57

Again we note, in this low coefficient of variation, a rather consistent character which will justify an investigation of species differences. Of course it may be said that a thorough examination of dispersion has been made in only one species and it may not be true that all species are equally consistent. Such large series, especially with all individuals carefully preserved and measured under uniform conditions, are not available in other species; and the method of computation is a rather laborious one. However, 41 other species, subspecies, and geographical groups were plotted and there was evidence of a comparable narrowness of dispersion.

The first use to which the correlation tables of these two large series are put is an analytic study of linearity. We calculate the eta coefficient of determination and, comparing this with the Pearsonian coefficient of determination, find them practically equal. Using the method of Fisher we find that the regression is not significantly curvilinear, F being below the 5 per cent level in both cases.\* The conclusion may therefore be definitely drawn that a straight line substantially fits the H-L relationship in this species. As I have stated elsewhere, a visual survey of the regressions of the other species justifies the opinion that this relationship is general among the rattlesnakes.

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\* Fisher, Statistical Methods for Research Workers, 4th Ed., 1932, p.237; Yule and Kendall, An Introduction to the Theory of Statistics, 1937, p.455; Davies and Yoder, Business Statistics, 1937, p.379.



The coefficient of variation given in the tabulation above is the average dispersion about the regression line on a percentage basis. An important question has to do with the trend in this dispersion--are juveniles more, or less, variable than adults, and is the difference conspicuous? This has been touched upon before, but we now have available complete sets of data from birth to maturity in two homogeneous series. Dividing our material into 100 mm. body-length zones and calculating the coefficient of variation of each zone separately, we have the following table:

Length Zone, mm.	Specimens in Zone		Coefficient of Variation in Per Cent	
	Platteville series	Pierre series	Platteville series	Pierre series
200- 299	129	13	3.32	2.35
300- 399	100	146	2.88	2.72
400- 499	11	21	2.72	4.16
500- 599	120	69	2.91	4.28
600- 699	186	111	3.88	2.90
700- 799	211	114	3.30	3.75
800- 899	63	154	4.05	3.73
900- 999	13	73	2.40	3.19
1000-1099	-	14	-	2.96
Total or Average	833	715	3.36	3.37

It will be noted that the weighted average of the zonal coefficients of variation is in each instance somewhat below the general average for the series as a whole, as set forth in the previous tabulation.

Because of the fluctuations between zones, the trend of the coefficient of variation is not clearly in evidence. To determine this trend the straight line of best fit, for these coordinates of the body length (L) and the coefficient of variation of H ( $V_H$ ), was determined for each series by the method of least squares with the following results:

$$\begin{aligned} \text{Platteville Series } V_H &= 0.000818L + 2.886 \\ \text{Pierre Series } V_H &= 0.000981L + 2.717 \end{aligned}$$

In order that the meaning of these equations may be more clearly visualized, we set forth the values of  $V_H$  at various body lengths, as derived from the equations:

	Values of $V_H$		
	L = 250 mm.	L = 500 mm.	L = 900 mm.
Platteville Series	3.09	3.30	3.62
Pierre Series	2.96	3.21	3.60

Thus we see (as is evident from the constants of the equations) that the trend of the coefficient of variation is to increase slightly as the snakes increase in length. In other words the dispersion of H about the regression line becomes somewhat greater with age and we have demonstrated that, in this species at least, young rattlers are less variable than adults--not only less variable on a basis of absolute measurements, which might well be assumed, but less even on a basis of percentage deviation from the mean head size at any body length.

It appears to me that an analysis of the trend in the coefficient of variation in a problem of this type gives

a useful picture of the nature of change in a body proportionality during ontogeny. This differs from the method of Harris\* where the trend in the proportionality itself is determined. The latter, it seems to me, is evident from the regression equation, for where the correlation is linear a negative value of Harris'  $r_{xz}$  merely proves that  $b$  in the equation  $X = aY + b$  is positive. In the present instance we have:

	<u>Platteville</u>	<u>Pierre</u>
	<u>series</u>	<u>series</u>
Pearson coefficient of correlation $r_{lh}$	0.989	0.988
Harris coefficient of correlation $r_{lz}$	-0.914	-0.931

Since  $r_{lz}$  is negative we know that H is a decreasing proportion of L, as L increases, which we knew originally from the positive value of  $b$ . Thus the Harris method does not appear pertinent in the present case.

So much for the directional trend of dispersion; we return once more to its character, that is, the shape of the dispersion surface. Taking our complete arrays of equivalent head lengths at a standard body length, we have the following statements of dispersion in terms of percentage of the mean head length:

<u>Percentage of Mean</u>		<u>Number of Specimens</u>	
<u>Class Limits</u>	<u>Class Center</u>	<u>Platteville</u>	<u>Pierre</u>
Below 89.5	-	1	3
89.5- 90.5	90	1	1
90.5- 91.5	91	3	3
91.5- 92.5	92	10	4
92.5- 93.5	93	14	10
93.5- 94.5	94	21	22
94.5- 95.5	95	38	45
95.5- 96.5	96	55	48
96.5- 97.5	97	79	59
97.5- 98.5	98	87	80
98.5- 99.5	99	97	76
99.5- 100.5	100	103	89
100.5- 101.5	101	84	85
101.5- 102.5	102	84	65
102.5- 103.5	103	52	48
103.5- 104.5	104	36	25
104.5- 105.5	105	24	17
105.5- 106.5	106	19	19
106.5- 107.5	107	12	4
107.5- 108.5	108	7	5
108.5- 109.5	109	1	1
109.5- 110.5	110	2	1
Above 110.5	-	3	5
		833	715

These distributions were compared with the distribution under the normal curve, by means of the chi-square test, with the following results:

<u>Series</u>	<u>Value of P</u>
Platteville <u>viridis</u>	0.893
Pierre <u>viridis</u>	0.226

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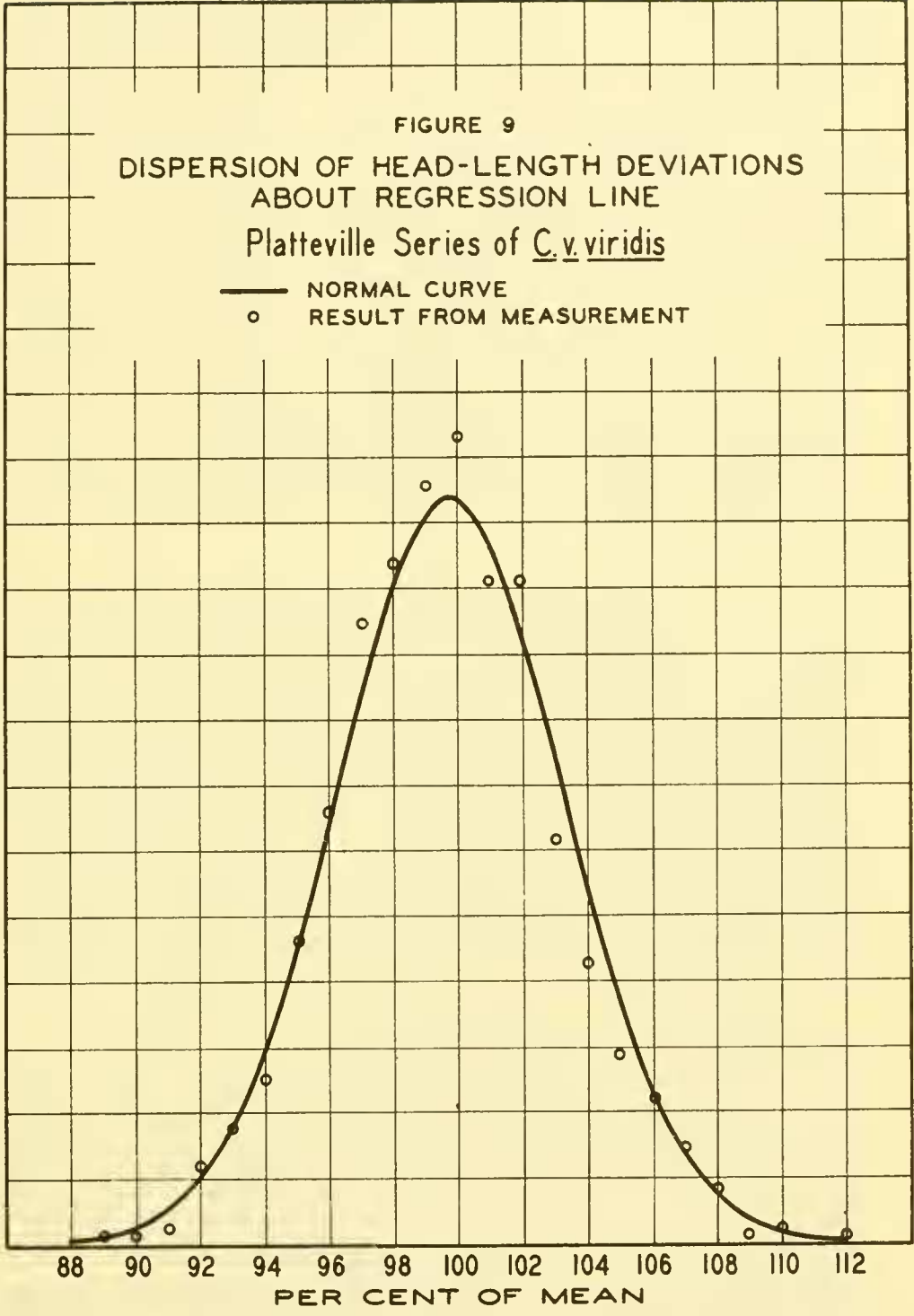
\* J. Arthur Harris, Biometrika, Vol.6, p.436, 1909; Genetics, Vol.3, p.328, 1918; Davenport and Ekas, Statistical Methods in Biology, Medicine and Psychology, p.95, 1936; Treloar, An Outline of Biometric Analysis, p.69, 1936.

FIGURE 9  
DISPERSION OF HEAD-LENGTH DEVIATIONS  
ABOUT REGRESSION LINE

Platteville Series of *C. v. viridis*

— NORMAL CURVE  
○ RESULT FROM MEASUREMENT

PER CENT OF SPECIMENS



Thus it appears that the distributions are probably normal. In order that the character of the adherence to the normal curve may be visualized, the situation in the Platteville series is given in Fig. 9.

It will be observed, both from the table on p.18 and from Fig. 9, that these distributions have a slightly negative bias; the means of the distributions instead of being 100 per cent are found to be 99.674 per cent in the Platteville and 99.550 in the Pierre series. This probably results from the original calculation of the regression lines having been made on a basis of absolute, rather than proportional, deviations. However, this is the only way in which  $b/a$  can be initially determined, and until this constant is known the method of translation to a standard body-size cannot be used. Based on the weighted trends in the deviation from 100 per cent in each length-zone, a correction can be made in the regression equation which will bring the mean to 100 per cent. In the Platteville series this correction is found to change the equation from  $H = 0.03553L + 6.968$  to  $H = 0.03552L + 6.891$ ; the corresponding correction in the case of the Pierre series is from  $H = 0.03350L + 8.363$  to  $H = 0.03336L + 8.329$ . The differences are of no practical importance and are only mentioned to indicate the source and correction of the deviation from 100 per cent. Since the zonal coefficients of variation were computed using the actual means, they are not affected by this slight error in the regression line.

Thus by a complete consideration of two large series of *C.v. viridis*, with respect to the head-length to body-length relationship, we have shown that (1) the correlation is linear; (2) the dispersion about the regression line is substantially normal; (3) the dispersion is nearly uniform on a percentage basis, increasing slightly amongst the adults, as compared with the juveniles. While we supply no analytic proofs beyond these series, our graphic surveys of forty other species, subspecies, and geographic groups indicate the same conclusions to be valid. There is no indication of subgeneric or group departures from linear regression, for there is as frequent a tendency to bow slightly above a straight line as to sag below it, and these departures seem to be the result of random sampling fluctuations. Similarly the proportionate type of dispersion seems to be indicated in all the available series.

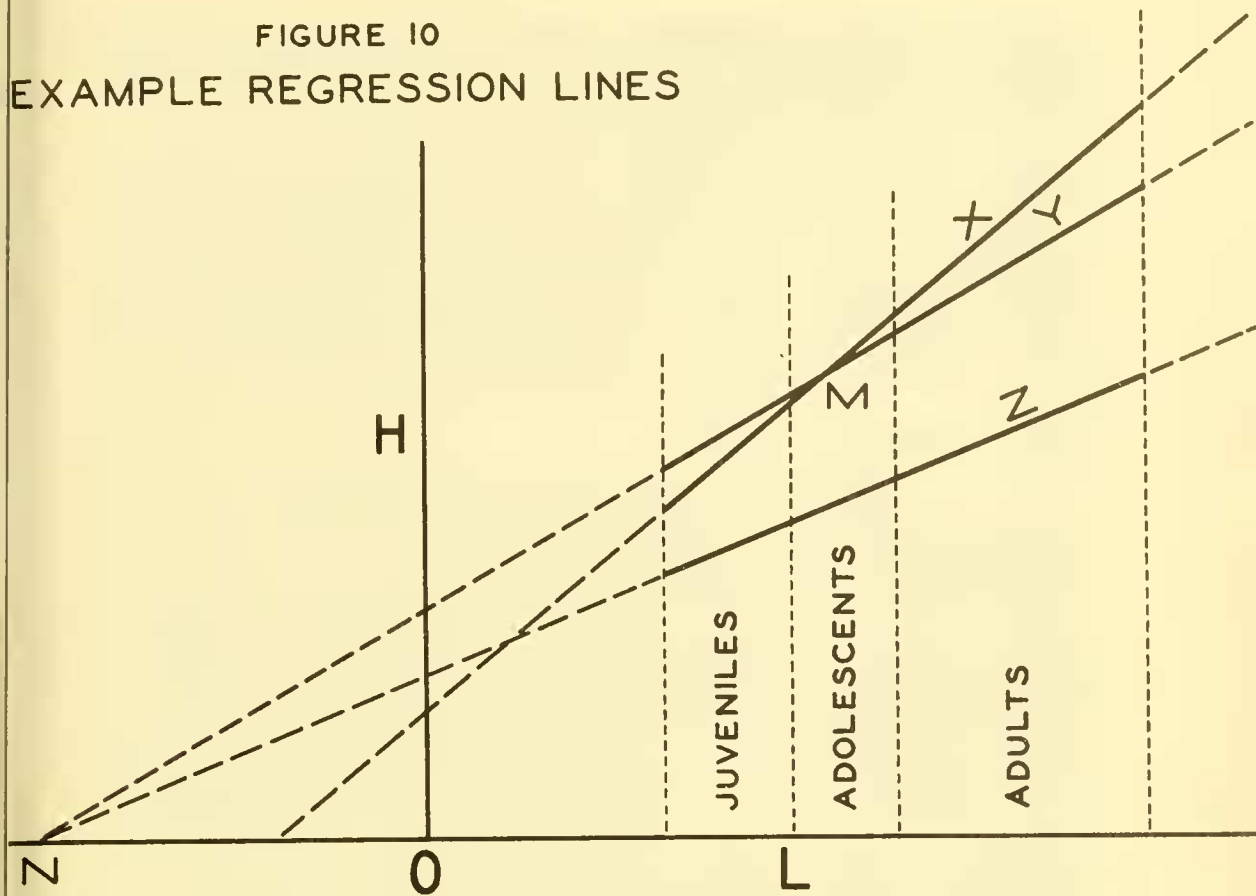
#### Head Length as a Diagnostic Character

Before proceeding to illustrations of the use of head-length statistics in taxonomy, it is advisable to discuss certain phases of the method which has been developed. Assume three subspecies to be investigated, and that the regression lines of their head-body relationships have been determined and are found to be the lines X, Y and Z as illustrated in Fig.10. Picture these as the back-bones or ridges of dispersion surfaces. The solid parts of the lines represent the range of length which each subspecies passes through in actual life; the dashed continuations are magnitudes either smaller or larger than the snakes ever attain in nature and are only included to illustrate points of intersection.

In choosing the specimens of any two groups to be

FIGURE 10

EXAMPLE REGRESSION LINES



compared we find ourselves faced with conflicting alternatives. The accuracy of the parameters of an unknown population is improved by having large samples; therefore we should use as many specimens as possible in our calculations. On the other hand, we have already pointed out that a wide range (in length) of specimens tends to accentuate errors resulting from any or all of the following: (1) inaccurate location of the regression line; (2) incorrect character of the regression line, e.g., curved, rather than straight, as assumed; or (3) inaccuracy of the theory that deviations from normal remain constant as percentages during life. Furthermore, assume that two species have regression lines which intersect in the adolescent range, as X and Y intersect at M in Fig.10. It is clearly evident that if we should happen to choose a standard length at M as a basis of comparison, the means would be equal and we would inevitably find the difference below the level of significance. On the other hand, if the two lines intersect at or close to  $H = 0$ , as do Y and Z at N, then we will not meet with this difficulty, and the choice of the length-limits of the individuals to be compared will be less important.

Having all of these considerations in mind it will usually be advisable to restrict the specimens compared to the available adults within a rather narrow length range. In cases where head length is of real importance in taxonomy, this is the range in which the difference should be demonstrated statistically, for we should naturally give more weight to an adult difference than to a juvenile difference that tends to disappear in later life. The two forms must

be snakes growing to about the same ultimate length; if one form is known to be smaller, or stunted, we must use certain special calculations to separate the mere effect of dwarfing from the real specific difference, if there be one. (See p.34). I shall return again to the head characteristics of stunted races, as compared to the forms from which they have been derived, and will show that they do not normally follow the same regression lines as their prototypes. To summarize: by taking a narrow adult length range, the statistical accuracy which we sacrifice by limiting our investigation to fewer specimens, is more than counterbalanced by the elimination of possible errors involved in translating specimens over too great a distance along their regression lines.

### Example Taxonomic Problems

We now proceed to work out some taxonomic problems involving head length to demonstrate the application of the method previously developed.

As we observe in captivity several cages of Crotalus mitchellii, some from the Cape Region of Lower California, others from San Diego County and western Arizona, it appears that the Mexican snakes have proportionately smaller heads than those from California; whether there is a difference between the San Diego County and Arizona material is uncertain. It is desired to determine whether these are real differences, or whether they are only imagined by the observer. Such differences, if present, are often more apparent in live than in preserved specimens.

We first survey the available material and find that moderately plentiful series of adults from each area are available. It appears that we can restrict the range to be included in our comparison to snakes no less than 700 nor more than 950 mm. in body length and still have adequate numbers. We decide on an approximate midpoint, or 850 mm. as the standard length at which the geographical groups will be compared. We now determine the regression equation for each group.\* With some experience this can usually be done graphically with sufficient accuracy to satisfy the necessities of this problem. To illustrate the method of transposing a head length to a standard body length, let us take an individual snake, a mitchellii from San Diego County with a body length of 755 mm., and a measured head length of 35.2 mm. It is desired to find the hypothetical head length at our arbitrarily selected standard body length of 850 mm. From a study of the available specimens from San Diego County, we first determine the regression equation to be  $H = 0.038L + 6.85$ , that is,  $a = 0.038$  and  $b = 6.85$ . Then  $b/a = 180$ .  $L_0$  is 850, and  $L_0 + b/a$  is 1030. From the formula  $H_0 = H (L_0 + b/a)/(L + b/a)$  we have the equation  $H_0 = 35.2 (1030)/(755 + 180) = 38.8$ , which is the estimated head length in millimeters that our snake would have at the standard body length of 850 mm. Standardized head lengths, thus computed for each available specimen, are then gathered into an array (separate for each geographical group which we are investigating), and their statistics are computed in

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\* In determining this equation, I prefer to use all available specimens of whatever age, rather than only those in the restricted length-class being compared.

the usual way. In the example mitchellii problem, we have the following:

	<u>Cape San Lucas</u>	<u>Central Arizona</u>	<u>San Diego County</u>
Number of specimens	45	18	29
Body length range, mm.	732-939	700-943	730-931
Standard body length, mm.	850	850	850
Mean head length equated to standard body length, mm.	32.04	39.33	39.24
Standard error of the mean, mm.	0.224	0.220	0.339
Standard deviation, mm.	1.50	0.93	1.82
Coefficient of variation, per cent	4.7	2.4	4.7

Using the ordinary formula to determine the standard error of the difference between the means of the parent populations, we find, comparing the San Diego County with the Cape San Lucas specimens, that the difference between the means ( $39.24 - 32.04 = 7.20$  mm.) is more than seventeen times its standard error (0.412), which is, of course, highly significant. On the other hand, comparing the Arizona with the San Diego County specimens, we find a difference between the means of 0.09 mm.  $\mp$  0.411. Here the difference is only one-fourth of its standard error, and is, therefore, without significance. We reach the conclusion that, in head length proportionality, the Cape San Lucas specimens are significantly different from those of the other two areas (which do not differ from each other); and, especially if confirmed by other characteristics, at least a subspecific segregation is warranted. Thus, the revival of Cope's name pyrrhus for the southern California and Arizona specimens is justified.

We now pursue a similar method in two other controversial problems. Some herpetologists still fail to distinguish between Crotalus tigris of southern Arizona and Sonora, and the form which I have called Crotalus mitchellii stephensi, an inhabitant of east-central California and southern Nevada. These snakes differ in certain scale characters; notably, the latter has sutured supraoculars, while those of the former are entire. Ordinarily, no one would suggest that a character as cumbersome as head size is seen to be, should be employed in diagnosis, when other, more readily determined and evaluated differences are apparent. But in the present instance, where doubt has been indicated by the non-recognition of the new form in some check lists, let us see whether the head size (which seems to me to be notably small in tigris and normal in stephensi) will reinforce the other differences. Using only adult specimens, we have the following statistics:

	<u>Tigris</u>	<u>Stephensi</u>
Number of specimens	30	37
Body length range, mm.	615-815	610-796
Standard body length, mm.	700	700
Mean head length equated to standard body length, mm.	26.55	31.58
Standard error of the mean, mm.	0.165	0.241
Standard deviation, mm.	0.90	1.47
Coefficient of variation, per cent	3.41	4.65

From the above statistics we find the difference between the means to be 16.9 times its standard error. As a difference of only twice its standard error indicates, with a strong probability, that the difference is real, and not the result of a chance divergence in the samples, there can be no question as to the real and extensive difference in head proportionality between tigris and stephensi.

To cite one more example: The neglected species, scutulatus, which was so long confused with cinereous, is another case in point. These species differ in head scales, hemipenes, pattern, color, and other characteristics; yet even today scutulatus has not been universally recognized as valid. The head-size comparison lends additional force to the differentiation, for scutulatus has the smaller head. It appears desirable to compare Arizona scutulatus with Arizona cinereous, since the two forms occupy virtually coincident ranges in that state, and are not greatly dissimilar in size, and thus any difference which may be found cannot be interpreted as a mere territorial or racial divergence; the two forms are either identical or separate species. I have also included, for comparison with the Arizona cinereous, a Texas series of cinereous, to show that this method may be as useful in disclosing identities as differences.

	<u>Cinereous</u>		<u>Scutulatus</u>
	<u>Texas</u>	<u>Arizona</u>	<u>Arizona</u>
Number of specimens	30	112	115
Body length range, mm.	700-1100	700-1100	700-1100
Standard body length, mm.	900	900	900
Mean head length equated to standard body length, mm.	40.75	40.17	36.74
Standard error of the mean, mm.	0.328	0.137	0.142
Standard deviation, mm.	1.79	1.46	1.52
Coefficient of variation, per cent	4.4	3.6	4.1

From the above statistics we find that the Arizona scutulatus-cinereous means differ by 17.2 times the standard error of the difference, which is significant beyond any reasonable doubt; the Texas-Arizona cinereous ratio is only 1.61, and thus is of doubtful significance. The difference in the latter case is probably due to the different ultimate sizes to which this species grows in the two areas, as will be explained later.

#### Validity of Head Length as a Diagnostic Character

All of these cases show a significance ratio above 4. In the present instance, while any difference is of interest in showing relationship or subspecific trends, I would not say, arbitrarily, that a difference between the means of twice the standard error is significant, even though the chances are only 4.6 in 100 that a difference of this extent is the result of random sampling, rather than an actual difference of the parent populations. But any significance ratio above 4 (indicating about 6 chances in 100,000) may



certainly be taken seriously, for this margin will more than compensate for slight errors in the assumptions or in the graphic selection of the regression lines.

A study of the method will show that, when the arbitrarily selected standard length is taken as the approximate midpoint of a narrow length-zone, errors in the slope or position of the regression line are relatively unimportant. This line influences only the translation of points to a standard size; in such translations the increments or decrements of the actual measurements are relatively small, and errors in the regression line result in minor errors in increments rather than in the basic figure to which they are added or from which they are subtracted. However, it is essential that the two forms compared grow to approximately the same ultimate size. If they do not, certain further adjustments must be made, as pointed out in the discussion of dwarf races (p.34).

One may make a fairly good guess from a mere inspection of the regression lines whether the difference is likely to be significant, provided we know something of the nature of the variation about the regression lines. In the rattlesnakes the coefficient of variation of head length, when equated to a standard body length, has been found to be somewhat below 5 per cent. If about 25 specimens of each form are available, a difference of 2-1/2 per cent in the means of the head lengths is likely to approach significance. Five per cent, or 2 mm. in head lengths of about 40 mm., is almost certainly significant.

In considering the method thus far demonstrated, I fully realize its relative impracticability, since many specimens are required and the computations are laborious. But the fault primarily lies in the nature of the head-length proportionality, not in the method. It is unfortunate, for simplicity of calculation, that L/H is not constant throughout life; the fact remains that it is not, at least amongst the rattlesnakes, and we must be guided accordingly.

These complications in dealing statistically with head length, or head proportionality, as a taxonomic criterion may be taken as illustrative of the great advantage which herpetologists and ichthyologists have in their work of classification, as compared, for example, with mammalogists and ornithologists. For, in the finer classifications (i.e., species and subspecies), the latter are dependent largely on items of pattern, color, and the proportions of body parts; and these last are beset with the practical difficulties so evident in this head-length study, since these proportions usually do not remain constant during the life of a single individual. But the student of reptiles and fish has available a considerable variety of scale quantities and arrangements which can be counted; these are expressible as numbers and remain invariant during ontogeny. Thus, quantities are readily available in a form most useful for statistical study, particularly with respect to the significance of differences.

### Short Cut Methods

We have reason to believe that head length, involving skeletal proportions as it does, is a relatively

stable character. The narrow dispersion within a species or subspecies, bears this out. We should, therefore, put it to use, where other less certain differences are to be validated, even though it is not easily manipulated.

It must be remembered that these statistical methods only determine the probability that two populations differ in a certain character. They do not prove that the difference is real, but they may show such a high probability of reality that the taxonomist accepts it as proof, beyond any reasonable doubt. But the final acceptance is a matter of judgment, not proof.

Refinement of method, then, leads only to the strengthening of a probability. If we can devise means of simplifying the method, without too strongly affecting the resulting probability, we may still have a useful working tool. Even the rather involved procedure hitherto used would, I am sure, draw criticism from the professional statistician because of some of the assumptions and the method of development. But it is an approach to accuracy and at least it has been useful in demonstrating the nature of the head to body relationship, and the inaccuracy of comparing simple L/H ratios without restriction. After all, we should not accept a difference of this kind as warranting a specific or subspecific distinction unless the evidence of a single character is overwhelming, or unless there be the cumulative weights of several independent characters all pointing to the same conclusion. Thus, refinement of probability, in terms of the ratio of a difference to its standard error, to the second or third decimal place, is not the goal of a calculation of this kind. But we would certainly feel more justified in making the segregation if the ratio, by what seem to be fairly accurate methods, is found to be in excess of three than if it turns out to be less than one.

The first modification toward workability, which may be suggested in this method, is one which involves grouping and simpler calculations, rather than a change in theory. Take the two species or subspecies to be compared and plot the coördinates of each available specimen on quadrille-ruled cross section paper. Draw the regression line of each by eye. Divide the available specimens of each species into groups by length; 10 mm. intervals will usually be found satisfactory, as for instance, all the specimens from 840 to 849 mm., inclusive, fall into one group.\* Pick off from the regression line the normal head length at the mean body length of each group; thus, in the above example, pick off the head length corresponding to a body length of 844.5 mm. Then, in each group, determine the ratio of the actual head length of each specimen to this normal length. For example, assume that the normal head length, at a body length of 844.5 mm. is found, from the regression line, to be 38.4 mm.,

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\* If a large number of specimens are available, say over 100, it will be simplest to group and average, in drawing the regression line, instead of plotting individual specimens. Where there are many specimens and this method is used, the results of selecting the regression line by eye are quite accurate. Thus, in the Platteville series a graphic determination produced  $H = 0.0355L + 7.0$ , while a corresponding table resulted in  $H = 0.0355L + 6.97$ . The corresponding equations for the Pierre series were: Graphic  $H = 0.0333L + 8.3$ ; analytic  $H = 0.0335L + 8.36$ .

and that we have three specimens (in the 840-849 mm. body range) with head lengths measuring 36.6, 38.0, and 40.6 mm.; then the ratios to normal of these three specimens are respectively, .953, .990, and 1.057. Gather these ratios for all available specimens into one statistical array and compute the standard deviation and coefficient of variation. The mean will be close to 1.0 if the regression line has been properly located. From the criteria discussed on p.20, determine the standard length at which the two species under consideration are to be compared. From each regression line pick off the normal head length corresponding to the standard body length. From the known coefficient of variation for each species, as above determined, compute the standard deviation from the equation  $\sigma = VM/100$ . For example, if we decide to compare our two forms at a standard body length of 900 mm., and we find, from the regression line of one of our species, that the normal head length for a snake of that size is 40.4 mm., and the coefficient of variation is 3.2 per cent, then the standard deviation is 1.22 mm. Thus, we have (for one of the two species) both of the statistics necessary to evaluate the difference between the two species. Proceed similarly with the other species and then determine the ratio of the difference between the means to its standard error as the test of significance.

It is necessary to re-emphasize the desirability of limiting the individuals to be studied to a rather short adult length-range for reasons previously mentioned, although this limit need not be applied in determining the regression lines. The determination of what range to use is best found from a study of the regression lines and the availability of specimens, as shown by the points on which the curves are based. Usually the zone selected should be wholly within the adult range, since a difference in head proportionality in the adult stage (regardless of the juvenile situation) will be more impressive than a difference between juveniles which fails to be manifest later in life.

Another approximate method is to draw up a standard linear correlation table\* for each of the species, using a restricted length-range. From the resulting statistics calculate the two equations in the form  $H = aL + b$  and determine the difference in the normal values of H at a standard head length near the center of range. Use the two standard errors of estimate as standard deviations and thus determine the significance of the head length differences. The assumption thus introduced, that deviations do not vary with length, is not important if the length range is narrow. However, this method is equally laborious, and is not particularly to be recommended.

### Use of L/H Ratio

What may be said with respect to the use of the far simpler  $L/H^\phi$  ratio as a basis of comparison? The answer

\* For example, see Mills, 1924, p.378; Pearl, 1930, p.378.

$\phi$  This is a preferable form to the reciprocal H/L since it is easier to visualize "the number of times the head is contained in the body length," than the "ratio of head to body." But either may be used without in any way changing the discussion.

of course depends on the nature of the regression curve. Assuming a straight line relationship, in any genera of snakes in which  $b$  in the equation  $H = aL + b$  is relatively small, we can use the L/H ratio directly in our comparisons and all necessity for the complicated procedure of equating to a standard body length is obviated. This possibility should be investigated by plotting sample regression lines. But if  $b$  is found important (as is the case with the rattlers), then the use of the L/H ratio is only an approximation, for we would have variations of L/H even if the linear correlation between L and H were perfect within each species. (See Fig.8). However, if we restrict our specimens to a rather narrow body-length range, and if they are evenly distributed throughout that range, then moderately reliable results can be secured, especially if the true significance is well above the usually recognized border line of significance. But it must be remembered that it is not sufficient merely to determine the differences between the two averages of L/H; the significance of this difference must be determined also, by comparing the difference with its standard or probable error.

For an example we may take the 30 specimens of C. tigris and the 37 specimens of C.m. stephensi previously treated by the more elaborate method on p.23, and investigate the significance of the difference in their L/H ratios. We set these ratios, separately calculated for each specimen, in a pair of the usual statistical arrays and from them we obtain the following statistics:

	<u>Tigris</u>	<u>Stephensi</u>
Number of specimens	30	37
Body length range, mm.	615-815	610-796
L/H mean	26.38	22.40
L/H range	23.9-29.1	20.0-24.2
L/H standard error of the mean	0.423	0.173
L/H standard deviation	2.32	1.05
L/H coefficient of variation, per cent	8.79	4.70

From these statistics we find the difference of the means ( $26.30 - 22.40 = 3.98$ ) to be 8.6 times the standard error of the difference (0.465). This difference is therefore significant. The ratio thus determined (8.6) may be compared with 16.9 as previously found by the more elaborate method. It is seen that while significance is indicated in both cases, it is less marked when the approximate method is used. It will be noted that the coefficients of variation are increased, as compared to the more accurate method; this result is to be expected since a constant L/H ratio assumes a regression line with a different and less accurate slope than the straight line of best fit, and the points do not cluster as closely around the former line as the latter. With the precautions outlined, the simple L/H ratio seems to be entirely sufficient to prove the difference between these two species. But it must be remembered that in this instance the difference is so marked as to be almost self-evident; the simplified method would not be so reliable

in a more doubtful case. It is essential in using this method that snakes of the same ages be compared, as may be presumed if it be known that they grow to about the same adult length; otherwise a difference in L/H may merely prove that snakes of different ages have been compared, rather than the existence of a real difference.

To set at rest any doubt as to the importance of the variation of the L/H ratio within a single species, I present herewith the statistics of 200 snakes selected at random from the Platteville series of C.v. viridis, 100 being juveniles from 270 to 300 mm. long, the other 100 adults from 720 to 760 mm.

	<u>Juveniles</u>	<u>Adults</u>
Number of specimens	100	100
Body length range, mm.	270-300	720-760
L/H mean	16.85	22.48
L/H range	14.9-18.4	20.6-24.2
L/H standard error of the mean	0.0664	0.0674
L/H standard deviation	0.664	0.674
L/H coefficient of variation, per cent	3.97	3.00

The mean difference (5.63) is found to be about sixty times its standard error (0.0946). Thus, there can be no question as to the real difference between head-size proportionality in juveniles and adults, the significance of which is evident even without the formality of calculation. The lack of overlap is noteworthy; not a single juvenile has as large an L/H ratio as the adult having the smallest ratio. Of course this is only a roundabout proof of the importance of b. With this extensive difference within a single species at different ages, it is shown how useless it is to use so variable a ratio as L/H to demonstrate interspecies differences, unless the size range of the specimens considered be severely restricted. But this size restriction imposes the necessity of many specimens, otherwise the samples will be too small for reliability.

### Dwarfed Forms

What are the relationships between stunted races and their full sized relatives in their H/L correlations? Do the two tend to follow the same regression lines, or is there some other consistent relationship between their respective equations?

We have 5 pairs or couplets of these forms. Their taxonomic relationships are generally obvious from similarities of scutellation and pattern, and from territorial considerations. In each case the stunted form seems to be an offshoot of the larger. These pairs are as follows:

Crotalus cinereus and C. tortugensis. The latter is a stunted species found only on Tortuga Island, Gulf of California. It is obviously derived from C. cinereus of

the mainland. (See Bull.Zool.Soc.S.D.,No.6,1930).

Crotalus ruber and C. exsul. The latter is a stunted form found only on Cedros Island. Ruber is a mainland species of the Californias. (Op.cit.)

Crotalus viridis viridis and C.v. nuntius. Inter-gradation between these two forms is undoubted. The first is widely distributed in the western Missouri-Mississippi basin; the second is restricted to northeastern Arizona and, in its most extreme form, is found only in the basin of the Little Colorado River near Winslow. Specimens from this vicinity only were used in working out the correlation between these two forms. (For further data on the relationship between these subspecies see Trans.S.D.Soc.Nat.Hist., Vol.8, No.13, pp.75-90, 1935).

Crotalus viridis lutosus and C.v. concolor. The latter form is intermediate in several characters between C.v. lutosus and C.v. viridis, and is territorially related to both. For the purposes of the present discussion I have assumed it to be an offshoot of lutosus.

Crotalus v. oreganus (San Diego County) and Crotalus v. oreganus (Coronados Islands). The stunted island form is clearly a derivative of the larger snake on the adjacent mainland.

From our studies of series of snakes involved in these several couplets we find the coefficients in the equation  $H = aL + b$  to be as follows:

<u>Couplet</u>	<u>Values of a</u>		<u>Values of b</u>	
	<u>Parent</u>	<u>Dwarf</u>	<u>Parent</u>	<u>Dwarf</u>
Cinereous-tortugensis	0.0351	0.0315	8.7	8.1
Ruber-exsul	0.0374	0.0354	8.4	8.2
Viridis*-nuntius	0.0345	0.0324	7.7	7.3
Lutosus-concolor	0.0337	0.0321	7.5	6.7
Oreganus-oreganus (mainland-island)	0.0361	0.0367	8.2	7.4

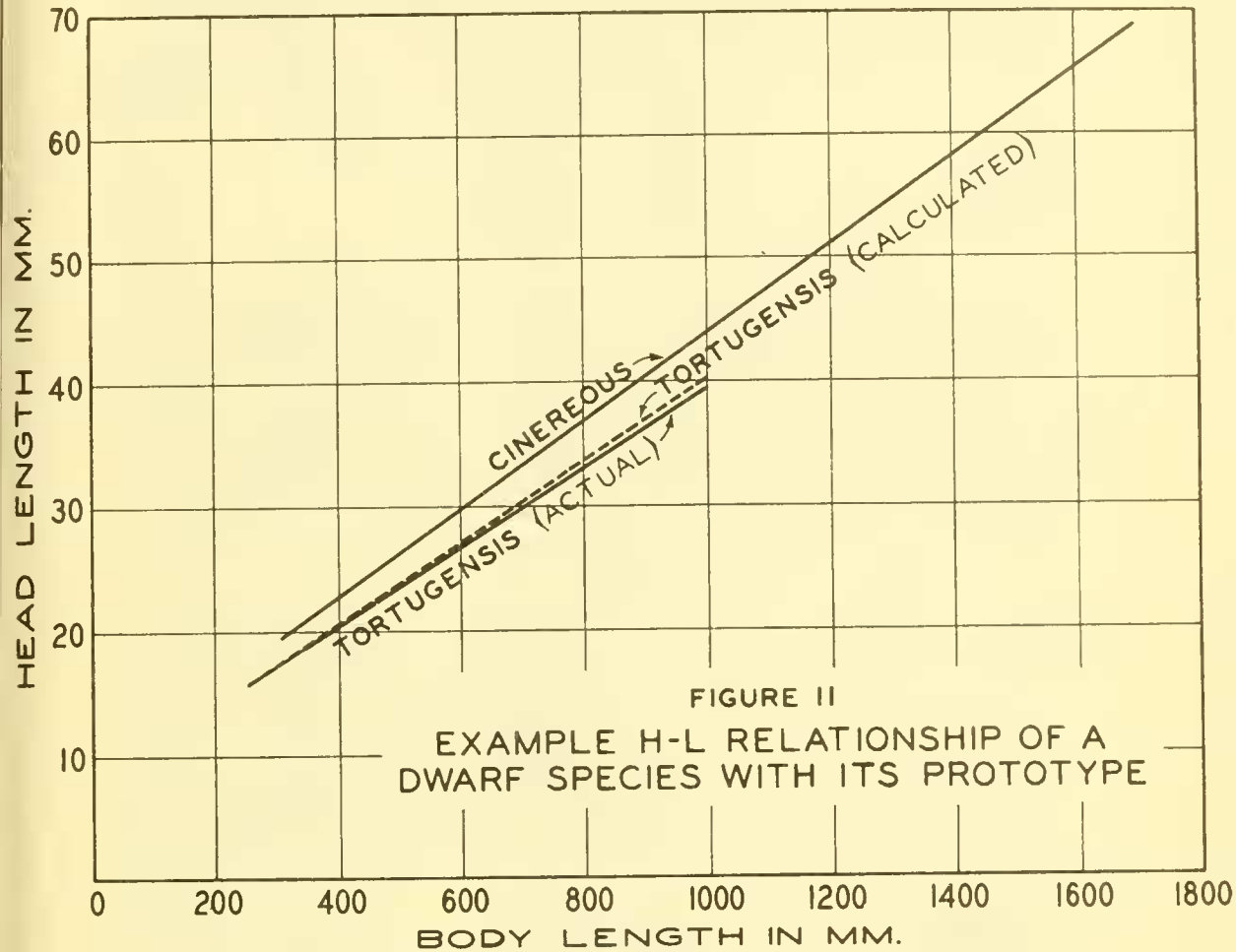
We note here a definite directional relationship, for in all but one case the derivative form has an equation lower in both constants a and b than the prototype from which it has presumably evolved.

An off-hand presumption might have led us to expect the two forms to follow the same H/L regression line. A brief consideration, however, will show that if two races are similar in body proportions at the same periods of life they must have different equations. For, assume two such races, one reaching approximately twice the average adult length as the other. Obviously, if the two follow a single regression line, an adult of the stunted form will have the head-to-body proportions of an adolescent of the larger subspecies. But we know from the previous discussion that young specimens have proportionately larger heads than adults; therefore, the two forms must follow different regression lines, unless dwarfed races have proportionately larger heads than their prototypes at corresponding ages.

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\* Average of Platteville and Pierre series.

Fig. 11 shows as an example the relationship of the regression lines of one of these pairs of species.



We next endeavor to find whether there is a fixed relationship between the equations of the couplets--whether there is any method whereby the equation of a stunted form may be determined from that of the prototype. We first test the head-length ratios at certain ages to see whether the dwarfs have the same ratios as their prototypes at the same period of life. If they do, we will have established a scheme of derivation. To illustrate the method of calculation, we take cinereous and tortugensis as examples. We start with the equation of the first as previously found,  $H = 0.0351L + 8.7$ . From Table 11 (see Occ.Pap.No.3,p.28) we ascertain that the average size of this form at birth is 310 mm., and the largest males are about 1700 mm. long. At these body lengths we find from the equation that the head lengths are 19.6 mm. and 59.7 mm. respectively. This gives L/H values of 15.8 at birth and 24.9 at full maturity.

We find from the same table that tortugensis is about 250 mm. long at birth and 1000 mm. at full male growth. Since this species is to have the same bodily proportions as cinereous, we apply the cinereous head ratios at these ages and find that tortugensis will have a head 15.8 mm. long at birth and 40.2 mm. at full maturity. From these two fixed points we determine the theoretical tortugensis equation to be  $H = 0.0325L + 7.7$ .

Similarly, the other couplets were tested and we find the following comparative figures for the constants in the equation  $H = aL + b*$ :

<u>Dwarfed Race</u>	<u>Values of a</u>		<u>Values of b</u>	
	<u>Actual</u>	<u>Computed</u>	<u>Actual</u>	<u>Computed</u>
Tortugensis	0.0315	0.0325	8.1	7.7
Exsul	0.0354	0.0358	8.2	7.1
Nuntius	0.0324	0.0332	7.3	5.8
Concolor	0.0321	0.0319	6.7	6.2
Oreganus (island)	0.0367	0.0336	7.4	5.8

We see that the results for constant a are moderately consistent with the facts but the computed values of b are uniformly low. Young specimens affect b more than a; from this it appears that a system of morphological similarity is not so closely followed in youth as in age. Of course the deviations may be the result of inaccurate assumptions with respect to average size at birth and at full maturity, for these affect the calculations. In some instances our supply of young specimens is quite inadequate to determine with accuracy either relative sizes or regression trends.

We may neglect the size at birth in our calculations by assuming another type of growth trend. We have seen that, in any single homogeneous group,  $H$  varies with  $L + b/a$ , rather than with  $L$  alone. Let us consider  $L + b/a$  as a sort of basic length of a snake, as opposed to its true length  $L$ . Assume further that dwarfed races have the same value of  $b/a$  as their parental analogues and that when the two forms are fully grown they are morphologically similar. What then would be the regression lines of the stunted races and how would these lines compare with those actually found from the specimens available? We have the following results:

<u>Dwarfed Race</u>	<u>Values of a</u>		<u>Values of b</u>	
	<u>Actual</u>	<u>Computed</u>	<u>Actual</u>	<u>Computed</u>
Tortugensis	0.0315	0.0323	8.1	8.0
Exsul	0.0354	0.0350	8.2	7.9
Nuntius	0.0324	0.0314	7.3	7.0
Concolor	0.0321	0.0309	6.7	6.9
Oreganus (island)	0.0367	0.0318	7.4	7.2

It will be observed that these calculated results agree more nearly with the facts than the assumption of morphological similarity throughout life, particularly with respect to the constant b. Considering the uncertainties of some of the basic data, the closeness of the actual and theoretical regression lines is rather striking. (See Fig. 11). I do not say that a correlation system has been proven, since the cases are too few, and the data too meagre to warrant such an assumption. It may be of interest, however, to consider what would be the relationship of regression lines and life stages in a group of related forms involving this

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\* Two sets of lengths are not obtainable from Table 11. These are the lengths of the Pierre and Platteville series of viridis, combined, which are assumed to be 250 mm. at birth and 1000 mm. for a large male; also the corresponding lengths of Coronados Islands oreganus are taken as 180 and 650 mm.



type of interrelation. Such a system is illustrated in Fig.12. If two forms of considerably different sizes are to be compared for taxonomic purposes, the amount of the difference that may be expected from size alone may be ascertained with a fair presumption of accuracy, by this method; and the remainder may then be assayed to determine the real species difference.

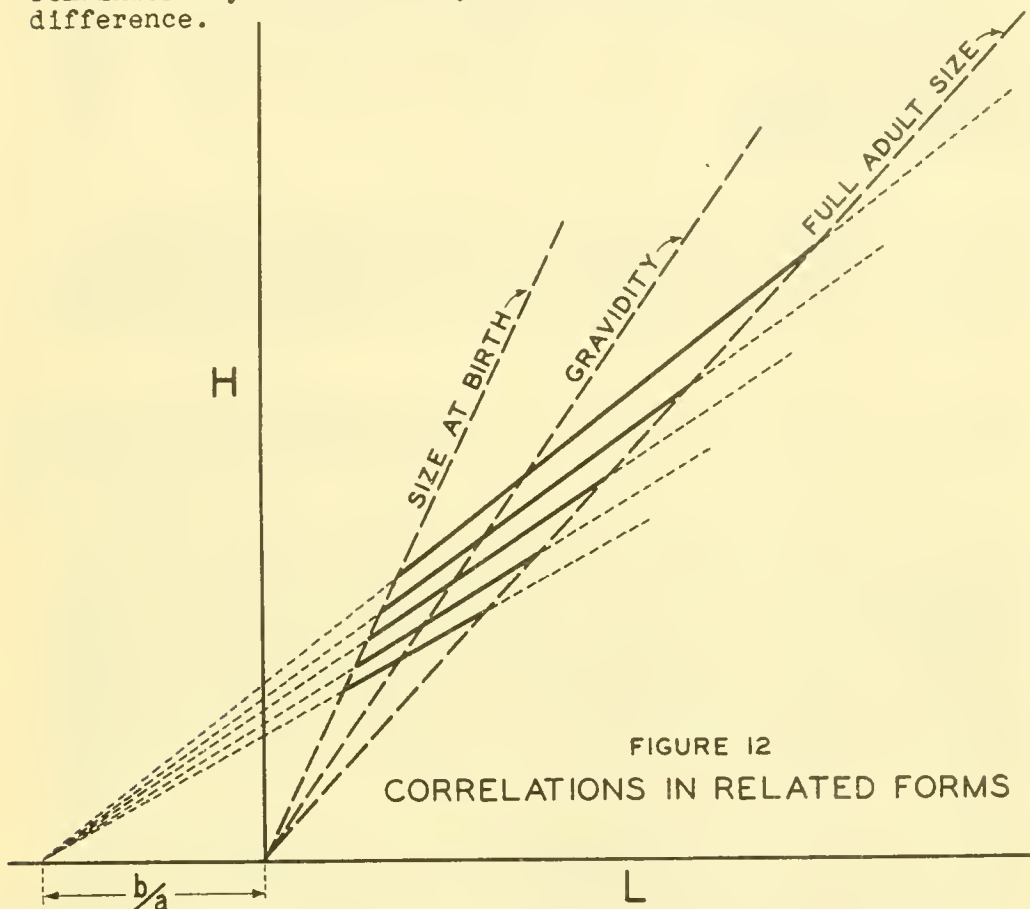


FIGURE 12  
CORRELATIONS IN RELATED FORMS

Possibly it may be deemed fruitless to attempt to find a formula wherewith to derive the regression curve of one of two related forms from the other.\* Disregarding this phase of the study, we have at least shown, by taking the actual curves representing the stunted races and comparing them with their prototypes, that the young of the dwarfed races have proportionately larger heads than their analogues when young, but that when the adult stage is reached morphological similarity is more nearly approached, although the dwarf head is still slightly larger in proportion to body

\* It may be thought that I have taken too much for granted in assuming that the larger form comprises the prototype from which the other sprang. As a matter of fact, the same geometrical relationship holds in either direction. We may, if we wish, assume the small forms to be ancestral, and calculate the regression curves of the large therefrom. However, this may be said concerning the rattler couplets: in every instance the smaller form is restricted in area (in three cases on small islands) and therefore comprises an insignificant population compared to the larger. More specimens of the large forms are at hand; their regression curves are therefore more accurately known and comprise a better basis of calculation.

length. This is shown explicitly by the following schedule:

Couplet	Values of L/H			
	At Birth		Large Male	
	Parent	Dwarf	Parent	Dwarf
Cinereous-tortugensis	15.8	15.4	24.9	24.6
Ruber-exsul	15.3	14.3	23.1	22.5
Viridis-nuntius	15.3	13.4	23.7	22.2
Lutosus-concolor	16.1	15.5	24.9	24.5
Oreganus-oreganus (mainland-island)	15.2	13.3	23.3	22.3

Here the dwarf juvenile ratios average 8.3 per cent lower than the parents; but the adult ratios differ by only 3.1 per cent. This corroborates the finding under growth,\* that stunting is not a uniform reduction from germ cell to adult, but is a force partly effective in the post-natal stage.

#### Effect of Ultimate Length on Species - Difference Calculations

I have previously stated (p.25) that, in making taxonomic comparisons, based on head length, it is necessary that the two forms have approximately the same total lengths over-all. If they are considerably different in size, we may be proving, in an exceedingly cumbersome manner, that one is a stunted race. For the proof of taxonomic difference, based on head length, is essentially the investigation of the separation of the two regression lines at some particular time of life--usually the adult stage. Having shown that stunted races have different regression lines from their prototypes, it follows that the same race in two areas, where different ultimate lengths are reached, will have different lines. In making comparisons for taxonomic purposes, we must be prepared to separate this factor from the total difference, to determine the amount attributable to a real morphological divergence. This presupposes some knowledge of the ultimate lengths to which the forms grow--a necessity which is obvious, for otherwise we cannot be sure that we are not comparing the adolescents of one form with the adults of the other. Such a comparison would lack significance.

We have seen that the relationship indicated in Fig.12 is closely followed by the stunted races which we have tested; it is also a rather logical assumption as representing the growth pattern of a single subspecies growing to different lengths in separate areas. While proof of this exact relationship is lacking, we believe it an approach to accuracy to compute from it the correction (attributable solely to length over-all) which should be applied to a difference before testing for significance. Calling the correction D, we have the following value as determined from the geometrical relationship of the variables:

$$D = H_1(L_0 + b/a)/(L_1 + b/a) - (H_1L_2/L_1)(L_0 + b/a)/(L_2 + b/a)$$

$L_1$  and  $L_2$  are the corresponding lengths of the larger and smaller forms, at some uniform-age basis of comparison, say a large male of each form as shown in Table 11.  $H_1$  is the head size of the large form at length  $L_1$  determined from the

\* Occ.Papers S.D.Soc.Nat.Hist.,No.3,p.31,1937.

known regression equation  $H_1 = aL_1 + b$ ;  $b/a$  is the ratio of the constants in the same equation, and  $L_0$  is the standard length at which the comparison is made (700 mm., for example, in the problem on p. 23, second table).

We now return to the three taxonomic problems previously discussed (p.22), and calculate D by means of the above equation, to see what effect this correction for ultimate lengths would have on the previous conclusions:

	<u>Pyrrhus-</u> <u>Mitchellii</u>	<u>Stephensi-</u> <u>Tigris</u>	<u>Cinereous-</u> <u>Scutulatus</u>
Total difference in head length at standard body length	7.20	5.03	3.43
Attributable to difference in length (value of D)	1.00	.80	2.70
Net real difference	6.20	4.23	.73
Standard error of difference (previously determined)	0.412	0.297	0.199
Significance	15.0	14.2	3.7

We see that the differences with respect to the first two pairs are still highly significant, the reductions being slight. On the other hand, in the cinereous-scutulatus couplet, the reduction resulting from adult length differences is more important, and the net separation of head lengths, although still above the border line of significance, has been decidedly reduced by the correction. Thus, this example indicates the importance of making an adjustment of this type.

However, it should be pointed out that the extent of the reduction in the scutulatus-cinereous comparison is partly the result of the large size (1700 mm.) assumed for cinereous, as compared with 1100 mm. for scutulatus. This is not really a fair basis of comparison. Over much of the central and northwestern sections of Arizona, cinereous is not as large a snake as in Texas, and the figure of 1700 mm. for a large male in Table 11 was based in part on Texas specimens. If we premise our conclusions exclusively on Arizona material we may use a length of 1350 mm. as being more fairly comparable with 1100 mm. for scutulatus. Also, we determine a new regression equation based only on Arizona cinereous, of  $H = 0.0350L + 8.3$ . Using these new data, we find the difference attributable to different ultimate sizes to be reduced to 1.30 mm. The net species difference becomes 2.13 and the significance 10.7, which thus validates the difference beyond any reasonable doubt. As I have pointed out before, this head length difference between scutulatus and cinereous is presented merely as an example. There are other conclusive differences, particularly of lepidosis, which can be demonstrated much more readily.

It might be thought that I have assumed too much in apparently taking for granted a racial or subspecific relationship between the forms being compared. As a matter of fact this has not been done. I have merely determined the difference (as an effect of relative size) which would naturally exist if one were a stunted form of the other, to see

if the remainder, which represents a true morphological difference, still retains significance.

### Effect of Ultimate Length on Dispersion

One more point remains to be mentioned. It is obvious from the fact that two races, one stunted (or gigantic) and one normal, do not follow the same head-length equations, that if we study a widespread population of a species, or subspecies, involving sub-populations reaching different ultimate lengths, the dispersion of the individuals about the line of regression will be greater than in a homogeneous series, because the several group-elements of the population really follow slightly different regression lines. Thus, even if the correlation in a local homogeneous population were perfect, a widespread population (assuming ultimate size differences) would show dispersion.

Carrying this further, it is evident that in a local population, having the usual variations in ultimate length common to all organisms, if  $L/H$  is to be a constant at any fixed age (full adult size, for example) then each individual must follow, during growth, a different regression line from his fellows. Thus, we have a tendency of uniformity in  $L/H$  to produce nonuniformity in  $H = aL + b$ . Furthermore, this would require the several individuals to approach the type of relationship indicated in Fig. 12, so that we have some theoretical reason to expect head length deviations from the rattlesnake mean regression line to vary with  $L + b/a$ , as was initially shown to be closer to fact than any assumption of a constant difference in  $H$  in terms of millimeters, or other absolute measurement.

We could test this theory without difficulty if we had a group of rattlers of assured age equality. As we have seen that stunted races do not closely follow their prototypes at birth in  $L/H$ , this test should be made upon adults. If we found in such a limited group that in their particular regression line the constant  $b$  tended to disappear, the theory would be proven. The sexes would have to be tested separately. With the material available, I have been unable to devise an accurate check of this relationship.

### Sexual Dimorphism in $L/H$

The theory of racial consistency in  $L/H$ , which has been indicated by the dwarfed species, would naturally lead us to expect the sexes to have different regression lines, since they reach different ultimate lengths, the males growing to a larger size than the females, except in cerastes. Our class comparisons (p. 3) failed to discover such differences. But if the sexes do have approximately the same regression lines, it follows that females have proportionately larger heads than males of similar age.

In order to check which of these relationships is more nearly adhered to (i.e., uniformity of regression, or morphological uniformity), we employ the Platteville series as an example. We assume that the largest males and females have reached the same average age. We take as representative of these groups, the 26 largest males (out of a total of 314 adults and adolescents) and the 24 largest females (out of

287), and find that we have the following data:

	<u>Males</u>	<u>Females</u>
Length range, mm.	860-949	791-857
Mean body length, mm.	899	814
Mean head length, mm.	38.3	35.9
Mean value of L/H	23.47	22.73

Now, if the females tend to have the same L/H ratio as the males, the average head size of the females should be  $814/23.47$ , or 34.7 mm. If, on the other hand they tend to follow the male regression line (which has been separately determined from the males alone) the head size would be 35.7 mm. Actually, the mean head size is found to be 35.9 mm., as shown in the original data. Hence it is clear that of the alternatives, the trend is toward the two sexes following the same regression line rather than morphological similarity at corresponding ages. Plotting the line which the females would have to follow, to be like the males in L/H at all ages, places the female line below actuality in every instance tested.

Another investigation of possible sexual dimorphism in viridis was made by the preparation of correlation tables of the Platteville and Pierre series, separating the sexes and using adults only. The regression equations were found to be as follows:

	<u>Platteville</u>	<u>Pierre</u>
Males	$H = 0.03326L + 8.25$	$H = 0.03229L + 9.25$
Females	$H = 0.03351L + 8.12$	$H = 0.03258L + 9.23$

It will be noted that in each instance a is slightly higher in the female equation than in the male; the contrary is true of the constant b. Taking snakes 900 mm. long and finding the head lengths from these equations, we find the sexual differences to be just below the level of significance. But, as the two series give the same result, I am inclined to believe that the difference is real, although of such slight magnitude as to be evident only in very large series. Our ignoring of sexual dimorphism in our calculations is still justified. These calculations are based on a coefficient of variation of 3.6 per cent, which figure has previously been found to represent the dispersion of the adults of these series.

From these two investigations we reach the conclusion that female rattlers of this species do not have the same L/H values as the males at corresponding ages. On the contrary, the sexes follow the same regression lines (or the female line may be very slightly above the male) which means that the females have larger heads at comparable ages. Less complete investigations of other races indicate the same conclusions, as did the original comparisons of average lengths by zones (p.3).

Crotalus cerastes seems to be the only species deviating from this normal rattler relationship, for it is the only species in which the males and females seem to follow different regression lines, the females having the larger heads at the same body lengths as the males. The difference is so considerable that it can hardly result from inadequate

TABLE 19

## CORRELATION OF HEAD LENGTH (H) WITH BODY LENGTH (L)

Equation  $H = aL + b$

Species	Number of Specimens	a	b	Values of H			Values of L/H		
				At 250 mm.	At 1000 mm.	At 250 mm.	At 1000 mm.	At birth	Large ♂
<i>C. durisus durisus</i>	49	.0346	9.4	17.9	44.0	14.0	22.7	15.9	24.9
<i>C. durisus terrificus</i>	19	.0349	9.3	18.0	44.2	13.9	22.6	15.3	23.9
<i>C. unicolor</i>	-	-	-	-	-	-	-	-	-
<i>C. basiliscus</i>	64	.0332	9.8	18.1	43.0	13.8	23.3	15.9	25.7
<i>C. enyo</i>	41	.0304	7.5	15.1	37.9	16.6	26.4	15.7	25.7
<i>C. molossus molossus</i>	114	.0395	7.1	17.0	46.6	14.7	21.5	15.5	22.0
<i>C. molossus nigrescens</i>	62	.0419	8.3	18.8	50.2	13.3	19.9	14.0	20.4
<i>C. adamanteus</i>	48	.0415	9.4	19.8	50.9	12.6	19.7	14.6	21.6
<i>C. cinereus</i>	412	.0351	8.7	17.5	43.8	14.3	22.8	15.8	24.9
<i>C. tortugensis</i>	44	.0315	8.1	16.0	39.6	15.6	25.2	15.6	25.3
<i>C. lucasensis</i>	333	.0375	8.9	18.3	46.4	13.7	21.6	14.6	22.5
<i>C. ruber</i>	224	.0374	8.4	17.8	45.8	14.0	21.8	15.3	23.0
<i>C. exaul</i>	16	.0354	8.2	17.1	43.6	14.6	22.9	14.4	22.7
<i>C. scutulatus</i>	298	.0316	8.7	16.6	40.3	15.1	24.8	15.8	25.3
<i>C. viridis viridis</i> (1)	1548	.0345	7.7	16.3	42.2	15.3	23.7	15.3	23.7
<i>C. viridis nuntius</i> (2)	96	.0324	7.3	15.4	39.7	16.2	25.2	13.7	22.9
<i>C. viridis sbyssus</i>	20	.0330	8.0	16.3	41.0	15.3	24.4	15.3	24.4
<i>C. viridis latusus</i>	311	.0337	7.5	17.9	41.2	14.0	24.3	16.2	24.9
<i>C. viridis concolor</i>	28	.0321	6.7	14.7	38.8	17.0	25.8	15.4	24.4
<i>C. viridis oreganus</i> (3)	839	.0350	7.9	16.7	42.9	15.0	23.6	15.7	24.0
<i>C. mitchellii mitchellii</i>	80	.0286	7.9	15.1	36.5	16.6	27.4	16.2	27.0
<i>C. mitchellii pyrithus</i>	173	.0371	7.0	16.3	44.1	15.3	22.7	15.8	23.0
<i>C. mitchellii stephensi</i>	59	.0350	6.8	15.6	41.8	16.0	23.9	15.4	23.3
<i>C. tigris</i>	38	.0244	9.1	15.2	33.5	16.5	29.9	15.4	28.0
<i>C. cerastes</i>	335	.0398	5.2	15.2	45.0	16.5	22.2	15.2	21.2
<i>C. polyactis</i>	19	.0340	8.4	16.7	42.4	15.0	23.6	14.5	23.3
<i>C. horridus horridus</i>	104	.0324	9.1	17.2	41.5	14.5	24.1	15.6	25.2
<i>C. horridus atricaudatus</i>	26	.0328	9.2	17.4	42.0	14.4	23.8	15.8	25.5
<i>C. lepidus lepidus</i>	15	.0355	6.5	15.4	42.0	16.2	23.8	14.6	22.0
<i>C. lepidus kluberi</i>	116	.0340	6.5	14.8	40.5	16.9	24.7	14.9	22.9
<i>C. triseriatus triseriatus</i>	66	.0368	6.7	15.9	43.5	15.7	23.0	13.4	21.0
<i>C. triseriatus pricei</i>	88	.0368	6.2	15.4	43.0	16.2	23.3	13.9	21.4
<i>C. stepheneri</i>	3	.0320	8.2	16.2	40.2	15.4	24.9	12.5	21.9
<i>C. willardi</i>	22	.0374	7.8	17.2	45.2	14.5	22.1	11.8	19.5
<i>S. ravus</i>	11	.0385	6.9	16.5	45.4	15.2	22.0	13.0	20.1
<i>S. miliarius miliarius</i>	47	.0343	7.0	15.6	41.3	16.0	24.2	12.8	21.0
<i>S. miliarius barbouri</i>	84	.0356	6.5	15.4	42.1	16.2	23.8	13.5	21.8
<i>S. miliarius streckeri</i>	65	.0357	7.1	16.0	42.8	15.6	23.4	12.7	21.2
<i>S. catenatus catenatus</i>	161	.0302	9.3	16.9	39.5	14.8	25.3	13.5	24.3
<i>S. catenatus tergeminus</i>	89	.0340	8.1	16.6	42.1	15.1	23.8	13.6	22.7

Total 6167

Notes: (1) Average of Pierre and Platteville series.  
 (2) From Winslow area only.  
 (3) Average of Pateros, Washington, and San Diego County series.

data. Nor is an explanation wanting. It will be remembered that this is the only species in which the females are consistently larger than the males (Occ.Pap.No.3,p.27). These two deviations from the rattlesnake normal appear interrelated. For it is evident that if males and females of normal species tend to follow the same regression lines, thus making the female heads proportionately larger at corresponding ages, we would expect that if a species developed larger females, and this head proportionality were retained, different regression lines would result, with a decided female superiority. This seems actually to have come about in cerastes. To show why this follows, let us take again as an example of the normal rattlesnake relationship the Platteville series of viridis. We have seen that at one age-equality (ultimate average growth) the L/H ratios are: males 23.47, and females 22.73; hence on this basis of age equality the female head will exceed the male in the ratio of 23.47/22.73, or about 3 per cent. The same proportionate condition occurs in other normal species of rattlers. Now, assume this relation to be maintained in a species in which the females grow to a length exceeding the males by 4 per cent, as is the case in cerastes. Then at equal lengths the two heads will differ by about 7 per cent and separate regression lines will result. This is approximately the difference in size between the heads of cerastes at an adult length of 650 mm. This relationship is subject to further verification as more adult specimens become available; the present investigation was based on 84 adult females and 135 males, but more very large specimens are necessary to smooth the curves. The approximate equations for cerastes with the sexes separated are: Males,  $H = 0.0391L + 4.9$ ; females,  $H = 0.0409L + 5.5$ . It will be noted that the differences in the constants are much greater than were found in viridis.

### Species Differences - General Discussion

I have placed the general discussion of species differences after that covering the position of dwarf forms, since the latter, if not first explained, would continually arise in any general comparison. I have endeavored to clarify the relationship which seems to exist, as a result of size differences, between the regression lines of related forms. Having disposed of this we may now proceed to a survey of the regression lines of H on L based on data available in all species and subspecies. These were set up on uniform coördinates and the values of the constants determined graphically.

The derived statistics are set forth in Table 19. The number of specimens measured, as shown in the first column, may be taken as some indication of the reliability of the regression constants.

A discussion of species differences and relationships, as indicated by these data, is beset with difficulties. The regression lines, although essential in any taxonomic determinations, do not in themselves, or in terms of their constants, permit species comparisons, or indicate subgeneric trends. And it is difficult to select a single quantity, or relationship, which may be readily used as a lucid basis of comparison. The employment of these regression lines is so intimately connected with considerations of age and size that their use is dependent on the availability of data with respect to the latter.

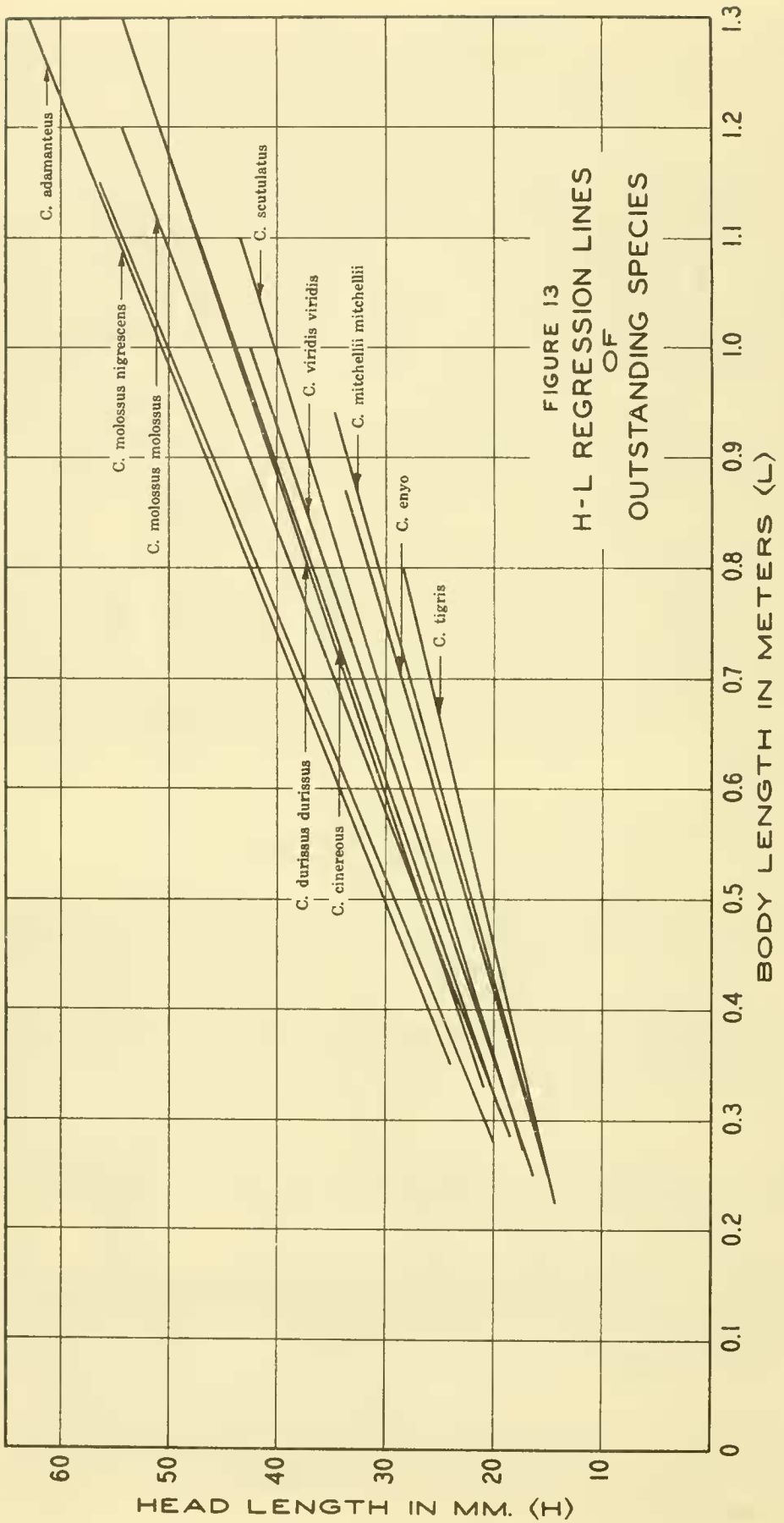


FIGURE 13  
H-L REGRESSION LINES  
OF  
OUTSTANDING SPECIES



In order that the relative locations of the species regression lines will be apparent I have presented in Table 19, for each form, the head sizes at 250 and at 1000 mm. A rather surprising uniformity is at once apparent. The juvenile heads range from a minimum of 14.7 mm. (concolor) to a maximum of 19.8 mm. (adamanteus). At a body length of 1000 mm. we have a range from 33.5 mm. (tigris) to 50.9 mm. (adamanteus). In the 1000 mm. series, out of 39 species and subspecies, only 6 fall outside of a range of 39 to 47 mm.: enyo, concolor, mitchellii, and tigris are low; while nigrescens and adamanteus are high. In the 250 mm. series the smallest head is 74 per cent of the largest; in the 1000 mm. series it is 66 per cent. Thus differentiation is greater amongst the adults. It is in this range that the results are both more accurate and more important.

Fig.13 shows the regression lines of a few of the more important species, together with those which deviate most conspicuously from the rattlesnake mode. The others cannot be shown, for the overcrowding in the vicinity of the cinereus and viridis lines would render the diagram illegible. Almost all of the lines not illustrated would fall within the narrow band between the molossus and scutulatus lines.

But these comparisons are of more interest in indicating uniformity of regression line trends than in suggesting species likenesses. For, in comparing the sizes of snake heads at a length of 1000 mm., we are introducing a certain fiction, since the smaller species do not attain this size. Nor would comparisons at 500 mm. be satisfactory, as this length, while representing the juveniles of some species, is within the adult range of others, and we have seen that the ratio is in part a function of time of life.

In order to afford a better basis of comparison Table 19 also sets forth the L/H ratios of each species at birth, and at the length corresponding to that of a large adult male, as taken from Table 11.\* This tends to compensate for the type of relationship shown in Fig.12. It is probably the best basis of comparison that can be devised. Necessarily the results are predicated on the accuracy of the data on the lengths at the two life periods, but this cannot be avoided. The same data are presented graphically in Figs.14 and 15.

The head-length ratios, thus determined, show a considerable consistency, both at birth and amongst the large sized males. At birth the larger snakes (from 220 mm. up) vary from 16.2 (mitchellii and lutosus) to 14.0 (nigrescens). Among the smaller species there is a definite tendency of L/H to vary directly with L; that is, the smallest species have proportionately the largest heads, ranging from 11.8 in willardi to 15.4 in concolor and 15.2 in cerastes. The same tendency is present amongst the larger species but is not so marked.

In the comparisons based on large adult males this

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\* Except viridis viridis, which, being a combination of the Pierre and Platteville series, is assumed to be 250 mm. at birth and 1000 mm. for a large male. Table 11 was based on Montana specimens.

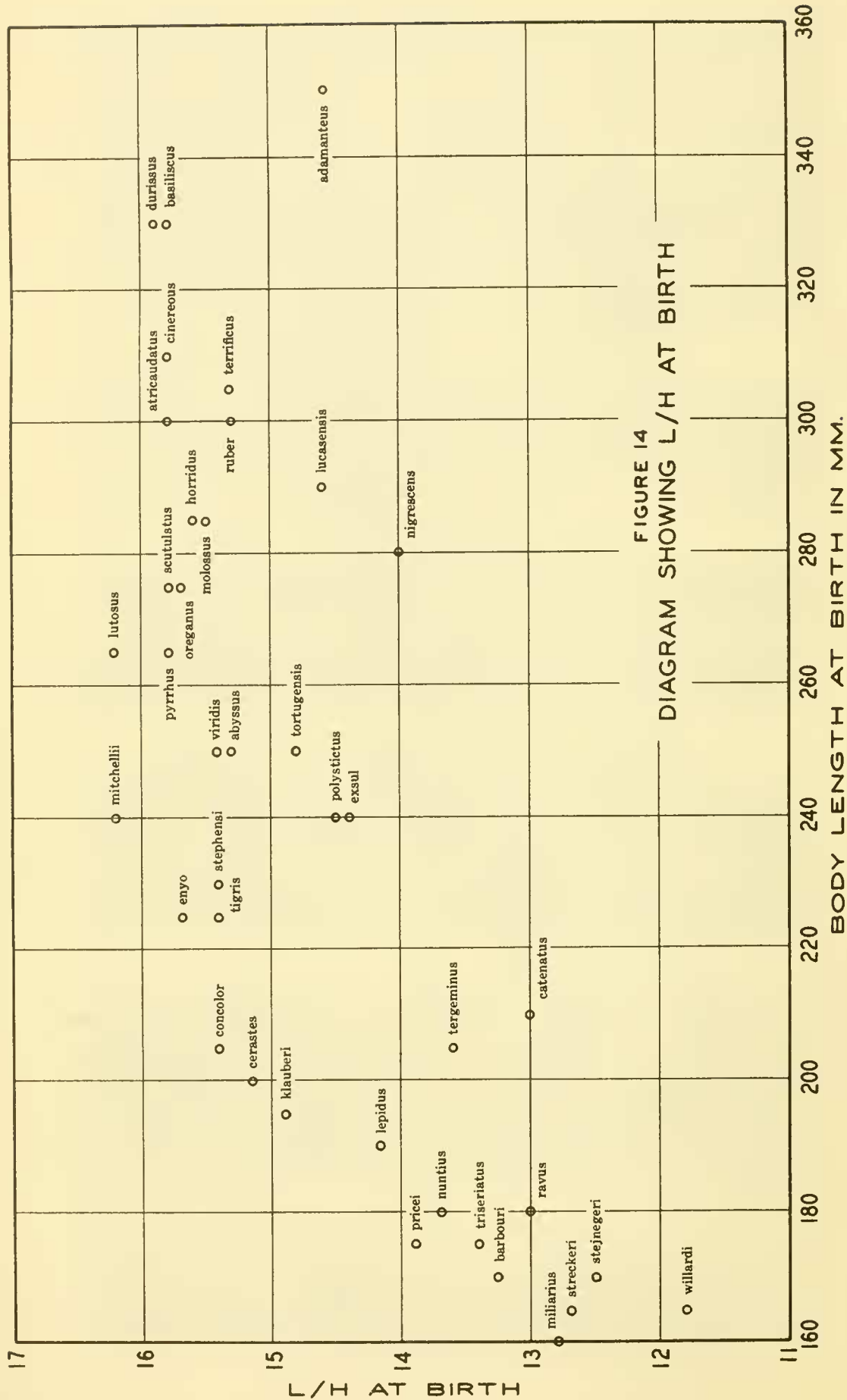


FIGURE 14  
DIAGRAM SHOWING L/H AT BIRTH

BODY LENGTH AT BIRTH IN MM.

tendency is again in evidence. Snakes having an adult length of less than 800 mm. have a well marked positive correlation between L/H and L; above this length the correlation is distinctly less evident and there are several exceptions to the rule. Among the latter the conspicuously small heads of tigris and mitchellii, and the large heads of nigrescens, molossus, and adamanteus are noteworthy.

A few group comparisons are of interest; these are based on the adult, rather than the juvenile L/H ratios; since the former are the more accurate and important. All of these comments are upon proportionality rather than absolute head size.

In the cinereous group, ruber and lucasensis have larger heads than their more widespread prototype. Adamanteus also departs from the normal of this group, having a very large head upon any basis of comparison.

In the viridis group there are no conspicuous deviates. While the smaller species have lower L/H ratios and therefore proportionately larger heads, the variations follow the rattlesnake mode. Lutosus has the smallest head of this group. Scutulatus shows a closer affinity to the viridis than to the cinereous group, a verification of the indications of certain other criteria.

Nigrescens and molossus, with large heads, are conspicuously different from durissus and basiliscus, to which they are often thought closely affiliated.

In the mitchellii group we have the greatest intra-group variation, tigris and mitchellii being conspicuously small-headed, while stephensi is normal and pyrrhus large.

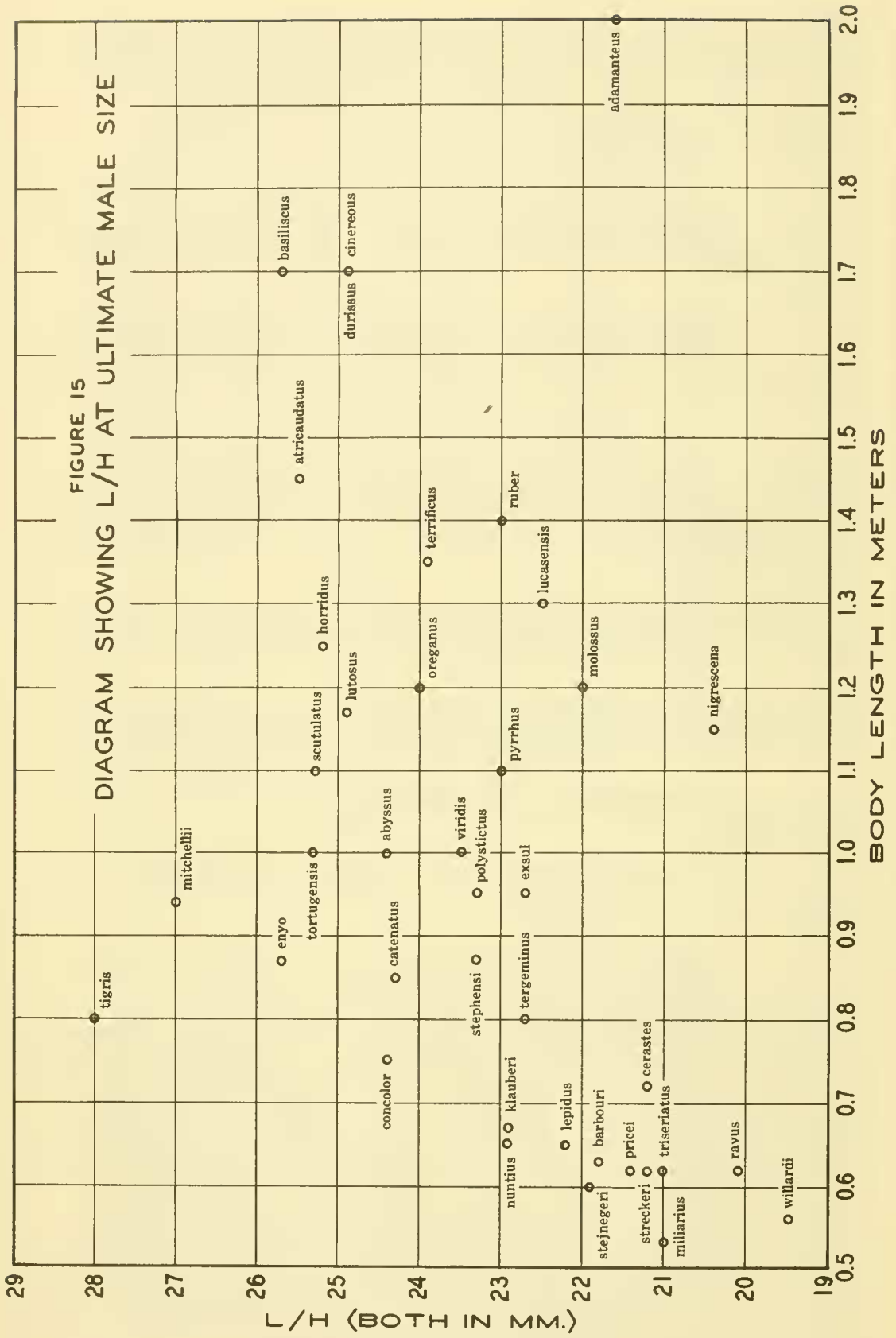
The triseriatus and lepidus groups have proportionately large heads but this is to be expected as they are all small snakes.

Of the Sistrurus species, ravus has a somewhat larger head than miliarius, and this in turn exceeds catenatus.

Summarizing general rattlesnake tendencies with respect to the correlation between L/H and L (not to be confused with individual species regression lines) we have, roughly, the following relationships between the size of any species and the relative size of its head: at birth (small species, 160 to 220 mm.),  $L/H = 0.073L + 0.46$ ; (large species, 220 to 350 mm.),  $L/H = 0.004L + 15.27$ ; large adult males (small species, 530 to 850 mm.),  $L/H = 0.020L + 9.0$ ; (large species, 850 to 2000 mm.)  $L/H = 0.0019L + 22.1$ . It should be understood that the scatter of the several species about these regression lines is considerable; the correlation is not particularly close, and the equations are only given to indicate trends, rather than to permit calculations of L/H, for these values are already available in Table 19. But there remains the undoubted conclusion that small species in general have proportionately larger heads than the larger species, and this is particularly marked in the smallest forms where the regression line is steeper, and adherence thereto closer, than among the larger species.

There are indications of a negative correlation

FIGURE 15  
 DIAGRAM SHOWING L/H AT ULTIMATE MALE SIZE



between head size and venom toxicity, upon which I expect to touch in a subsequent report. Thus, tigris and mittchellii, with the smallest heads, have the most powerful venoms among the rattlers; and ruber with the weakest venom, has an unusually large head and a correspondingly high venom yield.

### Width and Depth

It may be thought that I have given undue attention to the length of the head of the rattlesnakes, to the neglect of other dimensions, particularly the head width and depth. But it has been found that these other dimensions cannot be determined with the same relative accuracy as length. The length dimension is fixed by bone--by the distance from the face of the premaxillary to the posterior tip of the articular section of the mandible. But the depth and breadth are not so fixed, their boundaries being tissue. The result is that these dimensions are seriously modified by the conditions of preservation (by the extent of the pressure, and its direction, during the setting and storing periods), thus affecting the shape of the head and the ratios of the dimensions. Or, if the measurements be made before setting, the softness of the tissues are such as to make the results somewhat doubtful. The condition of the venom glands (whether full or depleted) modifies the head shape. Starvation in captivity would probably affect head width more than length. These limitations are unfortunate, as differences in head proportions are quite definite among the rattlesnakes--the slender head of polystictus and the flat head of pyrrhus for example--and were these dimensions measurable with a good degree of accuracy, criteria of interest in taxonomy would be available.

As it is, I propose to investigate in detail the relationship between head-length and width in a single series (the Platteville viridis) to determine the regression line of head width (W) on head length (H),\* and the nature of the dispersion about this line. But the investigations into the other forms will not be carried out to the same extent as was undertaken with respect to head length, since this is not justified by the data. However, a few species differences are pointed out, and the general conclusions from the Platteville series, with regard to changes in head shape during life, have been verified in other species.

A preliminary investigation of the W to H relationship in viridis, cinereous, and cerastes discloses no sexual dimorphism. Therefore, this possible additional complication is omitted from further consideration.

The head widths of 233 specimens of the Platteville series were measured while the specimens were pliable, prior to setting. They were allowed to rest on a table in a natural position while being measured, so that the results are probably as accurate as can be hoped for.

Starting as usual with a visual survey by plotting

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\* I use H as the symbol for head length, instead of any term involving the letter L, to avoid confusion with body length. Thus, H has the same meaning here as in the previous discussion of the relationship of head with body length.

Table 20

CORRELATION OF HEAD WIDTH WITH HEAD LENGTH: PLATTEVILLE SERIES OF C.y.viridis

Head Width in Millimeters

	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	Total
16		2	1																					3
17	2	12	9	1																				24
18		4	9	3																				16
19			3	4	1																			8
20				1	1																			3
21																								
22						2																		4
23																								
24							1	2	1		1													6
25							1	2	3		8	1												8
26							1	1																16
27								1	4	6	10	4	2	1										27
28								4	1	1	9	2	4	1										16
29												4												8
30												4												14
31														6	2	2								15
32														6	4	4								15
33														2	7	2	2							15
34															1	3	2							8
35															1	2	1							7
36															1	2	1			1				6
37														1	1	1								13
38																2	2	3	2	4	1			7
39																2	2	1	2	2	2			2
40																				1	3		1	5
41																				1	1			1
42																				1	1			1
Total	2	18	22	9	2	3	2	6	13	13	28	15	11	20	16	14	5	9	8	9	7		1	233

Head Length in Millimeters

the head width and length coördinates of our specimens, we find once more a straight line relationship,  $W = a'H - b'$ , but in this case  $b'$  assumes a negative value. (The accents are used to avoid confusion with the letters employed in the previous equations of the relationship,  $H = aL + b$ ).

Before proceeding with the detailed analysis of the Platteville data, it may be stated that this type of equation of  $W$  and  $H$  seems to be quite characteristic of the rattlers. Giving due regard to the scatter resulting from the difficulties of measurement previously discussed, in every case where sufficient material is available, a straight line of this type is clearly indicated.

Since the equation  $W = a'H - b'$  may be converted into  $W/H = a' - b'/H$ , and since  $b'/H$  is negative and decreases as  $H$  increases, it follows at once that  $W/H$  increases as rattlers grow. In other words, rattlers have proportionately wider heads as they mature; young rattlers have slimmer heads than adults.

Returning to the Platteville series of 233 specimens, a correlation analysis results in the following statistics. The straight line of best fit by the method of least-squares is found to be  $W = 0.808H - 2.55$ , both  $W$  and  $H$  being expressed in millimeters. The original data are presented in Table 20 as a visual exposition. The scatter is by no means excessive. The coefficient of correlation ( $r$ ) is high, being 0.982. This, however, is not of great importance, since it is self-evident that the larger snakes will have larger heads in both dimensions. The Harris correlation criterion,\*  $r_{hz}$  is 0.499. The standard error of estimate is 1.06 mm.

Since  $W = 0.808H - 2.55$  and from our former investigations,  $H = 0.0355L + 6.97$ , we can derive the equation of  $W$  and  $L$ ; this is found to be  $W = 0.0287L + 3.08$ .<sup>φ</sup> Hence, as in the case of head length, young snakes have larger heads (using the width dimension as a criterion) than adults. From these two equations we find the following proportionality in C.v. viridis between head length and width, at birth, and for a large adult male:

	<u>L</u>	<u>H</u>	<u>W</u>	<u>Ratio W/H</u>
At birth	250	15.9	10.3	0.65
Large male	1000	42.5	31.9	0.75

\* Treloar, op.cit., p.69.

φ It is obvious that these three equations are interrelated, for if  $H = aL + b$  and  $W = a'H + b'$  (in this particular case  $b'$  is negative), then the relation of  $W$  and  $L$  must be of the form  $W = a''L + b''$ . For if we replace  $H$  in the second equation with the value of  $H$  in the first, we have  $W = a'(aL + b) + b' = a'aL + a'b + b'$ . Thus  $a'' = a'a$  and  $b'' = a'b + b'$ , and any one of the three equations is obtainable from the other two. It is equally evident that we could have obtained the values of the constants  $a''$  and  $b''$  in  $W = a''L + b''$  from the original data at hand, leaving  $H$  entirely out of consideration. But being primarily interested in the head shape, that is, the ratio of width to length, rather than the ratio of head width to body length, I deemed it advisable to work directly with the relationship of  $W$  and  $H$ .

Table 21

## CORRELATION OF HEAD WIDTH (W) WITH HEAD LENGTH (H)

Equation  $W = a'H + b'$

	Number of Specimens	a'	-b'	W at H = 30	Values of W/H	
					At Birth	Large ♂
<i>C. durissus</i>	25	.84	5.0	20.1	.60	.77
<i>C. basilliscus</i>	25	.83	3.7	21.1	.63	.74
<i>C. enyo</i>	29	.78	3.1	20.3	.56	.69
<i>C. molossus</i>	62	.85	3.3	22.2	.67	.79
<i>C. adamanteus</i>	44	.83	3.8	21.0	.64	.76
<i>C. cinereous</i> (Arizona)	106	.84	2.8	22.3	.70	.79
<i>C. tortugensis</i>	47	.84	1.9	23.4	.72	.79
<i>C. lucasensis</i>	51	.83	3.6	21.2	.63	.75
<i>C. ruber</i>	135	.87	3.4	22.6	.70	.81
<i>C. exsul</i>	14	.85	3.4	22.0	.65	.77
<i>C. scutulatus</i>	152	.84	2.9	22.4	.67	.77
<i>C. viridis viridis</i> (Platteville Series)	233	.81	2.6	21.7	.65	.75
<i>C. viridis nuntius</i> (Winslow Series)	37	.86	3.5	22.4	.59	.74
<i>C. viridis abyssus</i>	15	.88	3.0	23.5	.70	.81
<i>C. viridis lutosus</i>	198	.87	2.8	23.2	.71	.80
<i>C. viridis concolor</i>	18	.80	1.1	23.0	.72	.77
<i>C. viridis oreganus</i> (Southern California)	73	.86	2.5	23.3	.72	.81
<i>C. viridis oreganus</i> (Coronados Islands)	18	.90	2.7	24.3	.71	.81
<i>C. viridis oreganus</i> (Pateros Series)	48	.82	1.9	22.8	.71	.78
<i>C. mitchellii mitchellii</i>	76	.96	3.7	25.0	.71	.86
<i>C. mitchellii pyrhus</i>	68	.92	2.8	24.8	.75	.86
<i>C. mitchellii stephensi</i>	45	.88	2.9	23.6	.69	.81
<i>C. tigris</i>	25	.81	2.4	22.0	.65	.74
<i>C. cerastes</i>	127	.90	2.1	24.8	.74	.86
<i>C. polystictus</i>	8	.64	2.2	17.0	.51	.59
<i>C. horridus</i>	34	.81	4.1	20.3	.59	.73
<i>C. lepidus klauberi</i>	64	.75	0.9	21.5	.68	.72
<i>C. triseriatus triseriatus</i>	21	.83	2.1	22.9	.70	.78
<i>C. triseriatus pricei</i>	55	.81	2.4	21.8	.65	.75
<i>C. willardi</i>	9	.75	1.7	20.9	.65	.71
<i>S. miliarius</i>	38	.72	1.1	20.1	.65	.69
<i>S. catenatus</i>	36	.81	2.8	21.5	.64	.74



Thus, we see in figures that, with this type of relationship, rattlesnake heads become proportionately wider as the snakes age; the young have slimmer heads than the adults. This same conclusion can be derived from a comparison of  $b/a$  with  $b''/a''$ . The latter figure is smaller, indicating that  $W$  is more nearly proportional to  $L$  than is  $H$ .

In order to prove that this trend is statistically significant, we compare groups of juveniles and young adults within narrow body-length ranges. A group of 40 juveniles varying in head length from  $16\frac{1}{2}$  to  $18\frac{1}{2}$  mm., were found to have an average  $W/H$  ratio of 0.665\*. Similarly, 26 adults having heads from  $35\frac{1}{2}$  to  $38\frac{1}{2}$  mm. long, average 0.740. Analysis shows the difference to be 6.7 times its standard error; therefore, there can be no question of its reality. The average body lengths of the snakes compared were: juveniles, 295 mm.; adults, 850 mm.

The coefficients of variation of the ratios were 4.7 per cent in the case of the juveniles, while the adult figure was 6.8 per cent. These quantities give an idea of the scatter about the  $W-H$  line.

We previously found (Table 18) that, in groups with narrow body-length restrictions, head lengths had a coefficient of variation of about  $2\frac{1}{2}$  to  $3\frac{1}{2}$  per cent in juveniles, and about 3 to 4 per cent in adults, this giving a good picture of the character of the scatter about the regression line  $H$  on  $L$ . A similar check on our Platteville series shows the juvenile dispersion of the head width about the  $W/L$  regression line to be about 5.1 per cent, and the adult 5.2 per cent. This wider scatter is probably due in part to a really greater variation in head width than head length, and in part to the difficulties of accurate measurement previously mentioned. It will be noted that in this measurement the dispersion is practically constant from youth to age on a percentage, not absolute measurement, basis.

So much for the analysis of a single species. This gives a sufficient picture of the extent of the variation of head width. We now turn to other forms to see whether there are important species differences.

In a number of species and subspecies, wherein good series of measurements were available, a graphical study was made to determine, separately for each form, the constants in the equation  $W = a'H - b'$  and other statistics of interest. The results are set forth in Table 21. Here are shown the values of  $a'$ ,  $b'$ , and the width-ratio  $W/H$  at birth and at ultimate male size. The value of  $W$  at  $H = 30$  mm. is also given, so that the direction of each regression line may be visualized. A few of these lines are shown in Fig. 16, which includes several species which adhere closely to the rattlesnake mode, as well as those which deviate most conspicuously therefrom. Most of those not shown would fall between the stephensi and adamanteus lines.

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\* The methods previously devised of equating to a standard head length was used; that is, each specimen was deemed to maintain a constant percentage deviation of  $W$  from the regression line, in translation from its actual value  $H$  to a standard  $H_0$ .

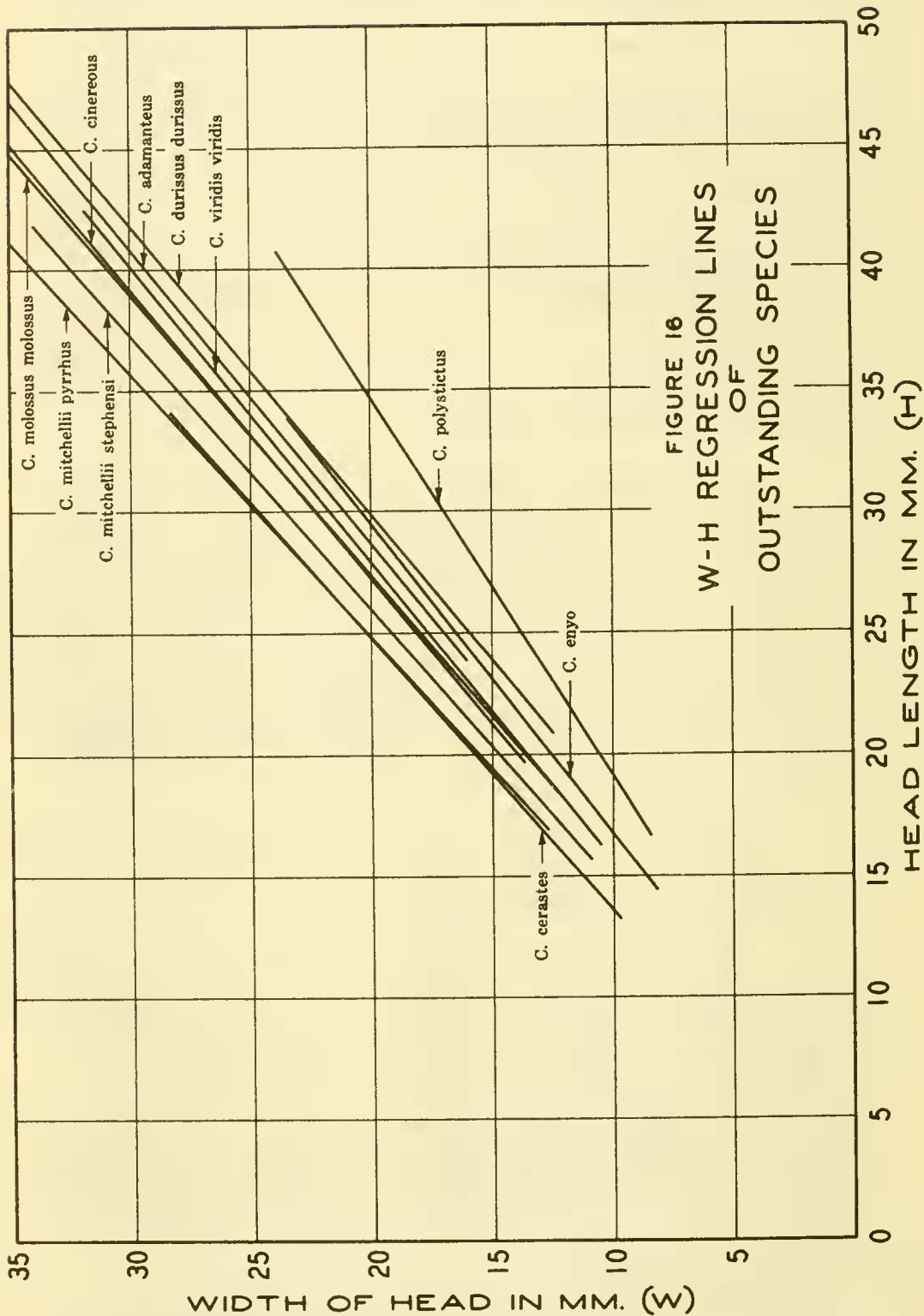


FIGURE 16  
W-H REGRESSION LINES  
OF  
OUTSTANDING SPECIES

We note here a certain uniformity in the equations; there are no great variations in the constants  $\underline{a}'$  and  $\underline{b}'$ . Particularly  $\underline{a}'$ , which is the more important of the two, is rather stable.

The constants  $\underline{a}''$  and  $\underline{b}''$  in the equation  $W = \underline{a}''L + \underline{b}''$  can be determined from the values of  $\underline{a}$  and  $\underline{b}$  given in Table 19 and the values of  $\underline{a}'$  and  $\underline{b}'$  given in Table 21, for we have shown that  $\underline{a}'' = \underline{a}'\underline{a}$  and  $\underline{b}'' = \underline{a}'\underline{b} + \underline{b}'$ . We will not discuss the equations of  $W$  and  $L$  except to repeat, as was stated in the viridis development, that, as  $\underline{b}''/\underline{a}''$  is always less than  $\underline{b}/\underline{a}$ ,  $L/W$  is more nearly a constant during ontogeny than  $L/H$ ; rattlesnake head widths are more nearly proportional to body length than are head lengths.

Just as the discussion of interspecies comparisons of head-length was difficult because of the changes during growth, so we find the same trouble here. Taking the rattlesnake mode to be represented by the important species viridis and cinereous, it will be observed that the head width is about 63 to 72 per cent of the head length at birth and increases to 74 to 83 per cent when full growth is reached.

Of those which do not follow this normal trend, polystictus is by far the most conspicuous, for it has a long narrow head;  $W$  being only 51 per cent at birth, and 59 per cent at maturity. Other species with narrow heads are enyo, millarius, willardi, klauberi, and horridus, in the order named, using the adult ratio as a basis of comparison. Nuntius tends to have the same  $W/H$  ratio as its prototype viridis at full growth; therefore its values of  $\underline{a}'$  and  $\underline{b}'$  are larger than those of viridis.

Mitchellii, pyrrhus, and cerastes are the only species having heads distinctly wider than the rattlesnake mode.

Head depth is even more difficult than width to measure accurately. Only three species were tested, cinereous, pyrrhus, and catenatus. Pyrrhus was thought to be particularly flat-headed and is, on a basis of width, but not length. The equations were found to be approximately  $D = 0.42H$  for pyrrhus,  $D = 0.44H$  for cinereous, and  $0.46H$  for catenatus. The scatter is considerable. At full growth the head depth in pyrrhus (using the  $W/H$  ratio previously found) is about 49 per cent of the width, while in cinereous it is 56 per cent. This difference was not as great as had been anticipated. Some of the smaller snakes have proportionately deeper heads. Thus, catenatus depth averages 62 per cent of the width. The indications are that the ratio  $D/H$  is more nearly constant amongst the rattlers than  $D/W$ . In other words, narrow-headed rattlers approach squareness when looked at head on, for although the head is narrowed proportionate to its length, the depth is not correspondingly reduced.

### Summary and Conclusions

1. Of the head dimensions of rattlesnakes, length is more accurately measurable than width or depth. This paper is primarily a study of head length ( $H$ ) in relation to body length over-all ( $L$ ).
2. Head length amongst the rattlesnakes, as

a proportion of length of body, is virtually independent of sex, except in C. cerastes. In this species the females have larger heads than the males of the same body length.

3. Among the rattlers the relationship of H and L conforms closely to a linear equation of the form  $H = aL + b$ . The constants a and b are in fairly close agreement among the several species. As b is always positive, juvenile rattlesnakes have proportionately larger heads than adults.

4. The straight line is the curve of best fit, there being no subgeneric trends deviating from this relationship. Variations in either direction away from a straight line appear to be dictated by chance.

5. Tests on six colubrid species indicate that two follow a straight line relationship, while four adhere closely to exponential equations of the form  $H = mn^L$ . Neither amongst the rattlers, nor these few colubrids, does any follow the simple ratio  $H = pL$ . From this it follows that  $L/H$  is not constant during life and interspecies comparisons cannot be made by comparing  $L/H$  except under restrictions with respect to corresponding ages.

6. In the rattlers the correlation between H and L is high, the correlation coefficient usually being well above + 0.85. However, as the dispersion is not constant in terms of absolute measurement, statistics other than the standard error of estimate must be devised in making comparisons.

7. The dispersion of H about the regression line of H on L is found to be practically constant on a percentage basis at all ages, although there is a slight increase in variability in the final adult stages. The coefficient of variation of H about the H-L line is usually between  $2\frac{1}{2}$  and  $3\frac{1}{2}$  per cent.

8. Based on constant percentage deviations, a method is devised for determining the equivalent head length at any arbitrarily selected standard body length. This permits the concentration of material for dispersion study. The distribution about the regression line is found to be substantially normal.

9. Since H has a coefficient of variation of about 3 per cent about the regression line, it constitutes a rather consistent character and may be useful in critical taxonomic problems, although such use is cumbersome compared with numerical characters (scale counts) which do not change during ontogeny. In using head length it is necessary to study the regression lines of the species being compared to determine at what length the difference should be ascertained. Usually, narrow ranges in L in the adult field should be adopted. The two forms being compared must grow to approximately the same ultimate length or a special correction is necessary, the formula for which is given. Example taxonomic problems are worked out.

10. Simple L/H ratios may be compared as a rough indication of differences. However, as the L/H ratio changes within any species during ontogeny, it is necessary to compare specimens at a rather restricted age.

11. The regression equations of dwarfed forms may be rather closely approximated by derivation from their prototypes. This derivation is based on a uniform L/H at maturity, and a uniform value of  $b/a$ , the ratio of the constants in the regression equation of the parent form.

12. Individual length differences in themselves tend to produce variations in  $H = aL + b$ , if the individuals are to have uniform L/H values at maturity. Thus, the dispersion of H about the H on L regression line may in part result from a tendency toward uniformity in L/H.

13. Species differences in H are pointed out. Tigris and m. mitchellii have conspicuously small heads; molossus and adamanteus large. Small species tend to have large heads; this is particularly marked in the smallest forms.

14. Studies of head width (W) indicate a straight line relationship with H,  $W = a'H - b'$ . An additional straight line relationship,  $W = a''L + b''$  follows from the two previously derived. The constant  $b'$  is always negative, hence adult rattlers have wider heads proportionate to head length than juveniles. Head widths are more nearly proportional to body length than are head lengths. The coefficient of variation of W about the W-L regression line is about 5 per cent.

15. Species comparisons with respect to W are presented. Most forms are found to have a W/H ratio of about 63 to 72 per cent at birth, and about 74 to 83 per cent at full maturity. Poly-stictus and enyo have conspicuously narrow heads; mitchellii, pyrrhus, and cerastes are unusually wide.

16. Head depth (D) is not measurable with great accuracy. In general, it seems to follow a simple ratio with H. D/H is more nearly constant amongst the rattlers than D/W. Thus, narrow-headed rattlers have deep heads compared to their widths, and wide headed-rattlers, such as pyrrhus, have notably shallow heads.